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CONTENTS.

ORIGINAL ARTICLES.

PAGE

BEATTIE, M. V. F.
The Physico-chemical Factors of Water in Relation to Mosquito Breeding in Trinidad (*illustrated*) 477

BONNE-WEPSTER, J.
A Mosquito with larval Habits like *Taeniorhynchus* (*illustrated*) ... 69
A remarkable Malformation in the Male Hypopygium of *Aëdes* (*Stegomyia*) *albopictus*, Skuse (*illustrated*) 233

BRUG, S. L.
Notes on Dutch East Indian Mosquitos (*illustrated*) 73
Chitinisation of Parasites in Mosquitos (*illustrated*) 229

CURRIE, G. A.
Oviposition Stimuli of the Burr-seed Fly, *Euaresta aequalis*, Loew (Dipt. Trypetidae) (*illustrated*) 191

DAVIES, W. MALDWYN.
Ecological Studies on Aphides infesting the Potato Crop (*illustrated*) 535

EDWARDS. F. W.
Mosquito Notes. XI (*illustrated*) 559

FAURE, J. C.
The Phases of Locusts in South Africa (*illustrated*) 293

GOLDING, F. D.
Sodium Fluosilicate as a Poison against the Hoppers of *Locusta migratoria migratorioides*, R. & F., in Nigeria 449

HARDY, G. H.
Notes on the *Sarcophaga peregrina* Group (Dipt.) 45
Some Australian Species of *Calliphora* (Subgenera *Neopollenia* and *Proekon*) (*illustrated*) 549

HODSON, W. E. H.
A Comparison of the Larvae of *Eumerus strigatus*, Fln., and *Eumerus tuberculatus*, Rond. (Syrphidae) (*illustrated*) 247
The Large Narcissus Fly, *Merodon equestris*, Fab. (Syrphidae) (*illustrated*) 429

JOHNSTON, H. B.
Notes on two Locusts of minor economic Importance in the Sudan 49

JOLLES, P.
A Study of the Life-history and Control of *Cerambyx dux*, Fald., a Pest of certain Stone-fruit Trees in Palestine (*illustrated*) ... 251

KING, H. H., & RUTTLEDGE, W.
On Experiments in the Use of Poison Dusts against Adult *Locusta migratorioides*, Rch. & Frm., in the Sudan 65

LEESON, H. S.
Methods of Rearing and Maintaining large Stocks of Fleas and Mosquitos for Experimental Purposes (*illustrated*) 25

PAGE

LE PELLEY, R. H.
Lygus simonyi, Reut. (Hem. Capsid.), a Pest of Coffee in Kenya Colony (*illustrated*) 85
On the Control of *Antestia lineaticollis*, Stål (Hem., Pentatom.) on Coffee in Kenya Colony (*illustrated*) 217

MACGILL, E. I.
The Biology of *Erythroneura* (*Zygina*) *pallidifrons*, Edwards (*illustrated*) 33

MACLAGAN, D. S.
An ecological Study of the "Lucerne Flea" (*Smynthurus viridis*, Linn.) I & II (*illustrated*) 101, 151

MER, D.
The Determination of the Age of *Anopheles* by Differences in the Size of the Common Oviduct (*illustrated*) 563

MILES, H. W.
Biological Studies of Sawflies infesting *Ribes* (*illustrated*) 1

MILLER, D.
The Biology and economic Status of New Zealand Muscidae and Calliphoridae.—Part I. Historical Review 469

MILLER, N. C. E.
Observations on *Melamphaus faber*, F. (Hem., Pyrrhocoridae) and Descriptions of early Stages (*illustrated*) 195

MYERS, J. G.
The original Habitat and Hosts of three major Sugar-cane Pests of Tropical America (*Diatraea*, *Castnia* and *Tomaspis*) (*illustrated*) 257

PICKLES, A.
Notes on the natural Enemies of the Sugar-cane Froghopper (*Tomaspis saccharina*, Dist.) in Trinidad, with Descriptions of new Species (*illustrated*) 203

POMEROY, A. W. J., & MORRIS, K. R. S.
The Tsetse Problem on the Eastern Cattle Route in the Gold Coast (With an Appendix by K. R. S. Morris on an Ecological Study and Experimental Clearing at Makongo) (*illustrated*) 501

SALT, G.
Superparasitism by *Collyria calcitrator*, Grav. (With an Appendix by R. H. Stoy) 211
The natural control of the Sheep Blowfly, *Lucilia sericata*, Meigen 235

TAYLOR, A. W.
Pupal Parasitism in *Glossina morsitans* and *G. tachinoides* at Gadau, Northern Nigeria (*illustrated*) 463

THEODOR, O.
On the Stucture of the Buccal Cavity, Pharynx and Spermatheca in South American *Phlebotomus* (*illustrated*) 17

UVAROV, B. P.
Ecological Studies on the Moroccan Locust in Western Anatolia (*illustrated*) 273

MISCELLANEOUS.

Collections received 147, 289, 425, 567

ERRATA.

Page 82, legend to fig. 11, *d* should read " scale of 8th segment of larva of *C. castrensis* " and *e* " scale on 8th segment of larva of *C. castrensis* var. *foliatus*, n., according to Senior-White "

,, 83, line 5, for " broader " read " narrower "

,, 224, line 11, and page 226, line 31, for " *Toxopterum* " read " *Toxoptera* "

,, 255, line 5, for " 15 cm." read " 15 mm."

,, 255, line 42, for " 17 cm." read " 17 mm."

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BIOLOGICAL STUDIES OF SAWFLIES INFESTING *RIBES*.

By HERBERT W. MILES, M.Sc., Ph.D.,
Victoria University of Manchester.

(PLATES I–V.)

BIONOMICS OF *Pteronidea ribesii*, SCOP.

Pteronidea ribesii, Scop., the common gooseberry sawfly, is widely distributed in Middle and Northern Europe and in North America, and appears to be confined to food-plants of the genus *Ribes*, particularly *R. grossularia* and *R. rubrum*. It has an extensive literature, one of the best and most recent accounts being that of Kemner (1924). In the present account, therefore, only a summary of the author's investigations are given, with emphasis on points of special interest or significance in relation to the present series of studies.

Habits of the Adults (Pl. i, fig. 3).

Imagines from overwintered larvae first appear in the latter part of April and continue to emerge over a period of three weeks or longer. They are active, especially in the sunlight of the forenoon. The males are restless and readily run or take to flight with the antennae vibrating rapidly. The females are rather less prone to flight. Mating, which has been described by Peacock,[6] was frequently observed in the laboratory, but not in the field. From observations on the insects in captivity, it would appear that mating depends on the more active habits of the male, since the female begins to lay eggs shortly after emergence, irrespective of mating having taken place.

On coming in contact with the food-plant the female runs rapidly from leaf to leaf, exploring the surface with palpi and antennae, and pausing frequently to test the ridges of the veins with the cerci (anal palpi of Kemner). When a suitable site for oviposition is located, the ovipositor is slightly protruded, the body arched, and the tips of the " saws " brought into contact with the leaf tissue. When the incision is prepared the egg is extruded and held in position until the release of the edges of the incision results in the egg being firmly gripped by the tissue. The time taken to prepare the incision and deposit the egg varies according to the age of the leaf, and while usually just over a minute, may exceed a minute and a half.

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The number of eggs laid by a female varies considerably, as the following table shows.

Table I.

Emerged	Died	Duration of life	No. of eggs laid
19 April	25 April	6 days	78
24 ,,	30 ,,	6 ,,	56
28 ,,	3 May	5 ,,	31
28 ,,	4 ,,	6 ,,	47
28 ,,	6 ,,	8 ,,	43
11 June	23 June	12 ,,	58
7 April	15 April	8 ,,	36
7 ,,	13 ,,	6 ,,	26

The figures in this table give an average of 47 eggs per female, which is higher than that obtained by Kemner,[3] who in 1923 obtained an average of 38 eggs per female.

Table I also gives the duration of imaginal life in a series of females. Observations on an equal number of males showed that the duration of life in male and female imagines of *P. ribesii* is practically similar, the average for each sex being 7 days.

The Egg Stage (Pl. i, fig. 4).

The eggs are laid in rows in small separate incisions along the main veins on the lower surface of the leaves. As many as fifty may be found along three or four veins of a single leaf, but under natural conditions 15–30 eggs on a leaf is more usual. The eggs are elliptical and measure about 1·2 mm. in length. When first laid they are pearly white and semi-transparent, but after a day or two they become cloudy and may assume a slight greenish tint. After five or six days from the time of oviposition the form of the larva can be discerned, and a day or two later the first suggestions of coloration are seen at the tips of the mandibles. These gradually become dark brown and distinct, and as the time of eclosion approaches, their movements can be detected through the chorion.

The period of incubation shows slight fluctuations, probably owing to the influence of temperature conditions, but appears to be between eight and nine days. Field notes support this, for males were first observed on the bushes on 3rd May 1929 and first instar larvae collected from the same bushes on 15th May. Allowing two or three days for the males to precede the females, this would indicate an incubation period of approximately 9 days.

The Larval Stage (Pl. ii, fig. 1).

At eclosion the larva of *Pteronidea ribesii* measures approximately 2 mm. It is at first pale, with the head smoky in colour. With the ingestion of green leaf tissue the body gradually assumes a greenish tint, but remains practically transparent, and the head darkens to a brownish black. Some markings are indicated as faint bluish areas of an indefinite character. The legs gradually darken, particularly in areas where the chitin is dense.

On hatching the larvae bite into the leaf tissue, and by the second day are feeding along the edges of minute circular holes dotted about near the veins, and giving the leaf a " shot-holed " appearance. By the third day they have usually reached the edges of the leaf, and when a number of larvae occur together they soon eat the leaf tissue, leaving only the main veins. They then proceed to another leaf.

About the fourth or fifth day after eclosion the larvae moult. In the second instar they assume faintly the typical coloration and spots, and adopt the feeding attitudes of the species. They feed along the edge of the leaves, with the caudal segments either curled under and forward or half curled and held slightly up off the leaf.

In 3-5 days after the first ecdysis the larvae undergo a second ecdysis. The characteristic spots and coloration are more pronounced in the third instar, and the larvae devour considerable quantities of leaf tissue. The third stadium lasts 4-6 days, and then a third ecdysis occurs.

The fourth stadium is variable. In the case of larvae that will become males it usually lasts seven or eight days, while in the case of larvae that become females it lasts only three or four days. At the end of the fourth stadium the larvae that become males cease feeding and undergo a fifth ecdysis. In the fifth instar these larvae are pale yellowish with microscopic setae, and without the black spots and long setae which characterise the preceding instars. The larvae that become females continue to feed during the fifth stadium, which lasts six days or even longer, and during which they retain the spots and colour usually associated with larvae of *P. ribesii*. At the end of this stadium they cease feeding and undergo a fifth ecdysis. In this prepupal instar they resemble the males of the fifth instar in that they are yellowish in colour and without the dark spots and long setae. In the prepupal stage of males and females no feeding takes place.

At each ecdysis the larvae assume a characteristic position, hanging head downwards from a leaf or petiole, which is firmly grasped by the caudal prolegs. The integument splits in the mid-dorsal line of the prothoracic segment, and the line of cleavage extends forwards along the epicranial suture to the frons and backwards over the thorax. Forward writhing movements push the exuviae backwards until the thorax protrudes, then the head is gradually freed from the old capsule and the rest of the skin worked quickly backwards over the abdomen. The time required for ecdysis is usually about ten minutes.

Immediately after ecdysis the larvae are pale yellowish green with a faint band of orange in both the thoracic and caudal regions. In a short time the setae with their black bases again become prominent, and the main body-colour darkens to a greenish-grey with a suggestion of orange on the thorax and the tip of the abdomen, and the head becomes dark brown or black.

The following table indicates the fairly regular development of the larvae.

TABLE II.

Date of hatching	Duration of Stadia					Total	Sex
	1st	2nd	3rd	4th	5th		
	days	days	days	days	days		
29 April... ...	5	3	4	8	—	20	♂
5 May	5	4	4	7	—	20	♂
5 ,, ...	4	5	4	8	—	21	♂
20 June ...	4	4	4	3	7	22	♀
16 April... ...	4	4	5	3	7	23	♀
14 May	4	4	4	8	—	20	♀
14 ,, ...	5	4	4	5	6	24	♀

The table shows that the larvae have three stadia of practically similar duration and a final feeding stadium which is longer than the preceding. It also shows the influence on the larval life of the sex of the subsequent adult. Larvae which become males have three short feeding stadia followed by a longer final stadium, while larvae

which become females have four short feeding stadia and one longer stadium, the average length of the feeding period thus being longer for the females than for the males.

The Prepupal Stage (Pl. ii, fig. 2).

After the final larval ecdysis, the fourth in the case of males and the fifth in the case of females, the larvae leave the bushes and enter the soil, where they construct cocoons. The cocoons are usually found in the top few inches of soil. They are oval, 8–10 mm. in length, and on the inner surface are of dark brown, parchment-like material, while on the outer surface there is a layer of adhering soil particles. The time spent in the cocoon prior to the pupal ecdysis varies considerably. In the case of the summer broods it extends over a period of from six to eight days, but the autumn brood larvae remain in the cocoons for over six months before pupation takes place. Occasionally larvae have been found to spend over a year in the cocoon.

The Pupal Stage (Pl. ii, figs. 3, 4).

The pupa is a pale yellowish-green in colour with a suggestion of deeper yellow or orange on the thorax and near the tip of the abdomen, and measures 7–8 mm. in length. The head is bent slightly forward so that the palpi lie on the anterior coxae, and the antennae lie in a curved position exterior to the wings and extending to the first or second abdominal segments. The prothoracic and mesothoracic legs are folded close to the ventral surface of the thorax, the tarsi of the mesothoracic pair reaching to the abdomen. The metathoracic legs are closely applied to the sides of the pupa, and the tips of the tarsi are free and capable of slight movements. The wings are sharply curved towards the ventral surface of the body, the anterior pair over-lying the tips of the posterior pair and reaching to the tips of the prothoracic tarsi.

The pupae appear restless in the cocoons, and those under observation were continually turning, the movement seeming to depend on a rotatory action of the abdomen.

The development of the pupa appears to be rapid and the adult emerges about seven or eight days after the pupal ecdysis.

Duration of the Life-Cycle.

A summary of the data in the preceding paragraphs indicates the length of the life-cycle. Under laboratory conditions the period from egg to adult in the case of the summer broods varies from 45 to 51 days, with an average of approximately 49 days; but under field conditions, where variations are greater, it may be shortened by several days. In the overwintering broods the life-cycle may require from six months to over a year.

The Cycle of Generations in Pteronidea ribesii.

Under natural conditions there seem to be three fairly well marked generations of *P. ribesii* per annum. In captivity adults from overwintered larvae emerged during the last week of April and the first week of May. Eggs were laid within a day or two of emergence, and by the end of May and the beginning of June the first generation of larvae was fully fed. Adults emerged from about the third week in June and gave rise to a second generation of larvae, which ceased feeding after about 31 days from the time the eggs were deposited. Adults again appeared about mid-August, and the third generation of larvae matured in September and early October. The data regarding generations were checked by supplementary observations in the field, which indicated that this was the normal annual cycle of generations.

Under laboratory conditions where the history of individual larvae could be traced, it was found that besides the normal annual cycle of three generations there

were individual variations which resulted in the occurrence of only one or two generations in the year. These variations were indicated by the emergence of adults long after the maximum emergence period for their particular generations. In some cases adults did not emerge from overwintered larvae until into June, and these gave rise to only two generations of larvae during the season. Occasionally development was retarded in larvae of the first generation. The normal emergence period for adults from this generation is the latter part of June, but it was found that some individuals failed to emerge until the end of July or the beginning of August. These gave rise to only one subsequent generation, which matured about mid-September, rather earlier than those of the normal third brood. Another variation from the normal development of the larvae of the first brood occurred when emergence as adults was delayed until the following year, in one case as late as June, thus rendering some individuals univoltine. With larvae of the second generation, which normally emerged as adults about the middle of August, development was occasionally retarded, and adults did not appear until the following year.

As a result of these observations it would appear that while usually there are three generations of *P. ribesii*, in certain circumstances variations may result from the retarded development of individuals and only one or two generations may be produced in the year. These variations probably account for the fact that under natural conditions larvae of *P. ribesii* can usually be found from May until early October in almost any district.

In the diagram on p. 15, the normal annual cycle of generations in *P. ribesii* is expressed graphically, together with individual variations in so far as they have been observed.

Proportion of Sexes and Seasonal Variation.

Parthenogenesis is characteristic of *Pteronidea ribesii*. The species is normally arrhenotokous, only mated females producing females. As a result of this there is considerable variation in the proportion of the sexes both from generation to generation and from year to year.

Wild larvae collected in several localities in Cheshire in the autumn of 1927 produced in the spring of 1928 a preponderance of females (5 : 1). Taking this as an indication of the proportion of sexes under field conditions, it would suggest that many of the females emerging in the spring of 1928 would be unmated and would therefore reproduce parthenogenetically. This would result in a preponderance of males in the summer brood. The females of the summer brood would be mated, consequently the late summer brood would consist of both sexes with the possibility of females predominating. This would influence the third generation of larvae and tend to favour the production of males from larvae overwintering in 1928–1929. That this occurred was indicated by a predominance of males (9 : 1) in wild larvae, and in the field in the spring of 1929 considerable numbers of males were found on the wing but comparatively few clusters of spring brood larvae were found subsequently in the same localities. Autumn-caught larvae produced a preponderance of females (4 : 1) in the spring of 1930. This would suggest that under conditions prevailing in the north-west of England there is a biennial cycle of alternating sex predominance.

Further observations have indicated that the predominance of either sex is local rather than territorial; for in 1929, when males predominated in Lancashire and Cheshire, females appeared to predominate in Gloucestershire.

Kemner[3] in Sweden has paid some attention to the cycle of alternating sex predominance. He states that he found females predominating in the second generation (June–July) of 1922, this pointing to a predominance of males from the overwintered larvae of 1921–1922. In the spring of 1923 he again records a predominance of males, though this is not consistent with his observations on the alternation of sex predominance. As a result of his observations Kemner suggests that males pre-

dominate in the spring and autumn and females in the summer, and indicates an annual cycle of generations: male, female, male. In this cycle the overwintering generation of larvae, in which females should predominate, produces males in the spring. The two years' cycle, indicated by the observations of the writer, affords a constant sequence of alternating sex dominance and would give males predominating in the spring broods of alternate generations.

Retarded development, which is a frequent phenomenon especially in the summer brood of larvae, tends to balance the sex ratio and thus would prove favourable to the continuation of the species.

The Bionomics of *Pteronidea leucotrochus*, Hartig.

Pteronidea leucotrochus, like the closely allied species *P. ribesii*, is found on the gooseberry, but occurs only rarely. It has, however, characteristics which are of special interest in parallel studies of the sawflies infesting the gooseberry.

Cameron,[1] who examined specimens from Clydesdale, Rannoch, York, Worcester and Lastingham, referred to the insect as "Seemingly not an uncommon species." An account is given by Ormerod,[5] based mainly on observations made in 1882 by one of her correspondents in Somerset. In 1909 Theobald[9] summarised the accounts given by both Cameron and Ormerod, but he appears to have made no original observations on the species and concludes his account with the following sentence: "Further observations are required concerning this species before anything definite can be said regarding its life-history."

The material from which the following information has been accumulated was obtained in Gloucestershire, where seven practically mature larvae were found feeding on an isolated gooseberry bush on 27th May 1928, and a further stock was obtained from the same bush the following year. Subsequently larvae were obtained from Huntroyde in Lancashire. Field observations have been supplemented by observations on the habits of the species in captivity.

The Habits of the Adults.

The habits of the adults of *P. leucotrochus* showed a close resemblance to those of *P. ribesii*, the insects running over the leaves and taking up moisture or resting in the shade. Of six adults of *P. leucotrochus* which emerged in 1929, a male died after four days and five females lived 17, 7, 8, 11, and 11 days respectively, or an average of 10–11 days, thus showing greater longevity than adults of *P. ribesii*.

As with *P. ribesii*, egg-laying began as soon as the newly-emerged female was placed on a gooseberry twig, and the attitude adopted was similar to that of *P. ribesii*. The time taken to lay an egg varied from 65 seconds to two minutes. Whereas, however, *P. ribesii* almost invariably selected the lower surface of the leaf and followed the line of the veins, *P. leucotrochus* placed eggs indiscriminately on either upper or lower surface of the leaf and showed no predilection for the veins as sites for the eggs, which were laid singly or in twos upon the leaves and well distributed over the twigs. In captivity a female confined on a twig bearing 27 leaves, laid eggs as follows: 1, 3, 2, 3, 6, 3, 1, 1, 6, 1, 6, 4, 4, 1, 3, 2, 3, 2, 1, on 19 leaves. The predominance of single eggs or small groups of two or three is well marked in this series. In the field no number higher than three was observed, but most frequently the eggs were placed singly. This confirms the observations recorded by Ormerod (*op. cit.*) that "only about three [caterpillars] hatched on each leaf." In the case of a second female confined on a twig, it was observed that 30 eggs were laid, and of these, 23 were placed on the upper surface of the leaves and only 7 on the lower surface (Pl. iii, fig. 2).

The number of eggs laid by a single female showed some variation, four kept in captivity laying 53, 30, 33, and 41 respectively. In captivity the oviposition period was often protracted, in one instance a female laying two eggs 15 days after emergence and a further egg on the 16th day, while at that time some of the earliest progeny were in the second instar. The greater longevity of the species may be accounted for by the fact that it does not lay a considerable number of eggs at a single oviposition as *P. ribesii* does, and may therefore be less liable to rapid exhaustion. Moreover the development of the eggs prior to oviposition may be less rapid than in the case of *P. ribesii*, for whereas successive batches of the eggs of *P. leucotrochus* took eleven days to hatch, those of *P. ribesii* required only eight to nine days under exactly similar conditions.

When first laid the eggs are translucent, pale creamy yellow and measure about 1·25 mm. in length. In about six days the faint outlines of the developing larva can be discerned, and a day or two later the brown tips of the mandibles become visible. The day before eclosion the mandibles can be seen opening and closing, apparently in an effort to rupture the chorion.

The incubation period of *P. leucotrochus* under laboratory conditions is 10–11 days.

The Larval Stage (Pl. iii, fig. 3).

On eclosion the larvae of *P. leucotrochus* bear a strong resemblance to the first instar larvae of *P. ribesii*. They are translucent white with a smoke-coloured head, and the eyes and tips of the mandibles are brown. After a few hours the lateral tubercles darken and appear fairly conspicuous. The length at eclosion is about 2 mm.

The feeding habits also resemble those of *P. ribesii*. For about three days after eclosion the larvae of *P. leucotrochus* feed in "shot-holes" within the periphery of the leaf, the margins remaining intact. Since only two or three larvae occur on a leaf, the "shot-holes" made by this species are much less conspicuous than those made by *P. ribesii*. By the third or fourth day the holes reach the leaf margins and the larvae then proceed to feed along the leaf edges, in the manner fairly typical of Nematid larvae. During this period the larvae remain pale in colour, but the head and the tips of the caudal sclerite gradually darken, the spots on the thorax become more pronounced, and tiny setae appear on both thorax and abdomen.

The first ecdysis occurs when the larvae are four days old. They cease feeding for a short time, then, gripping the edge of the leaf on which feeding took place, hang head downwards and slough the old skin. A few hours after the moult normal coloration is resumed. In the second instar the larvae have pronounced black spots, many of which are seta-bearing like those of *P. ribesii*. A faint yellowish colour is visible in the thorax and caudal region, but this is soon obscured by the green contents of the alimentary canal. The head gradually darkens until it is shining brownish-black.

During the first stadium the larvae grow rapidly and approximately double their length, so that at the first ecdysis they are about 4 mm. long. In the second stadium growth in girth becomes more apparent, and the larvae adopt the characteristic Nematid feeding postures, with tails either curved forward ventrally or lifted off the edge of the leaf and held in the air. At the ejection of the frass pellets the tail is suddenly thrown up and waved until the pellet is detached. The second stadium lasts about three days.

After the second ecdysis the yellow coloration of the thorax and caudal region is again fleetingly present. The setae with black bases are fairly conspicuous, but the spots are smaller and the whole body rather slighter than that of *P. ribesii* in the corresponding instar. On close examination the head is seen to be mottled, but the dark brownish-black coloration predominates. After the second ecdysis the larvae

measure about 7 mm. in length, and during the third stadium, which is three to five days in duration, they attain a length of about 10 mm.

After the third ecdysis the head is greenish in colour with dark blotches made up of small circular brownish areas. The dark areas on the body are fully developed, and when the larva is extended they appear similar in number and arrangement to those of the larvae of *P. ribesii*. The general coloration of the larvae of *P. leucotrochus* is, however, much softer than that of the larvae of *P. ribesii*, and the contrast between the black spots and the greenish body-colour is much less pronounced. The pale yellowish colour on the thorax and tip of the abdomen, which was evanescent at the first and second ecdysis, is continuously evident after the third ecdysis, and on the abdomen extends from the 8th segment to the tip. The caudal segment is somewhat globular, and the tips of the small brown cerci are distinct but not conspicuous.

During the fourth stadium sex differences become apparent. In the case of larvae that become males the fourth stadium lasts 7–8 days, and in the case of larvae that become females from three to four days. In the larvae that become females there is little difference between fourth and fifth instars except in size and colour emphasis of both integument and setae. During the final stadia growth in length and girth continues until a maximum length of about 15 mm. is attained.

In the later stages the larvae of *P. leucotrochus* can be distinguished from those of *P. ribesii*, being slighter in build and having paler heads, in which brown instead of black predominates. The body coloration is also less pronounced in *P. leucotrochus*, and whereas in *P. ribesii* the large lateral spots bearing setae are entirely black, in *P. leucotrochus* they are light brown, except at the immediate base of each seta where it is dark brown or black.

The Prepupal Stage.

As with *P. ribesii*, the prepupal ecdysis takes place at the end of the fourth stadium in larvae that become males, and at the end of the fifth stadium in larvae that become females. Since feeding is not resumed after this ecdysis, some details regarding ecdysis are more readily apparent. The chitinous intima of the stomodeum is shed with the head capsule and mouth-parts, and that of the proctodeum with the caudal region of the integument. The intima of the mesenteron, however, is shed independently about an hour or so after the detachment of the exuviae, the larva remaining quiescent until this has taken place.

In the prepupa the head is at first pale but later suffused with light brown. The eyes are black and the mouth-parts dark brown. The body is pale green with a slight yellowish tinge, which is most pronounced over the thorax and on the eighth and ninth abdominal segments. The integument is wrinkled into numerous folds, and though apparently free from the characteristic markings of the previous instars, microscopic examination reveals raised areas surmounted by short pale setae in the positions formerly occupied by black spots. During this instar the dorsal vessel is clearly visible through the integument and the rate of pulsation appears to average about 100 in 105 seconds.

Shortly after the prepupal ecdysis the larvae enter the soil, where they construct cocoons closely resembling those of *P. ribesii* in shape, size and colour. Seven cocoons measured 9, 8, 8·5, 8, 8, 8·5, and 9 mm. respectively. In the account given by Ormerod,[5] the larvae of *P. leucotrochus* are said to prefer nail-holes and holes in wood as sites for spinning the cocoons. From the observed habits of captive larvae of the species, this is abnormal, and it seems probable that the larvae found in these sites by Ormerod's correspondent were those of another species.

The Duration of Larval Life in Pteronidea leucotrochus.

The following table indicates the length of the feeding stages in *P. leucotrochus*.

TABLE III.

Date of hatching	Duration of stadia in days					Total no. of days	Sex
	1st	2nd	3rd	4th	5th		
	days	days	days	days	days	days	
18 April... ...	4	4	5	8	—	21	♂
18 ,, ...	4	4	4	3	7	22	♀
18 ,, ...	3	4	4	7	—	18	♂
19 ,, ...	4	5	5	7	—	21	♂
19 ,, ...	4	4	4	4	7	23	♀
1 May	3	4	3	6	—	16	♂
5 ,, ...	4	3	5	6	—	18	♂
19 ,, ...	3	2	2	7	—	14	♂
19 ,, ...	3	2	5	5	7	22	♀

The larvae of *P. leucotrochus* are fully fed in approximately three weeks after their eclosion from the egg. Like those of *P. ribesii* they have three short feeding stadia common to both sexes, and also a final feeding stadium which is much longer than the preceding ones. The sex of the subsequent adult influences larval development in a manner similar to that obtaining with *P. ribesii*, the larvae which become females having one short feeding stadium more than those which become males.

With the larvae of *P. leucotrochus* the time spent in the cocoon shows none of the variation which arises in *P. ribesii*, the period being from 338 to 340 days.

The Pupal Stage.

The pupa of *P. leucotrochus*, which closely resembles that of *P. ribesii*, measures 7 mm. in length and 2·5 mm. across the thorax. The body is greenish with a yellowish tint in the thoracic and caudal regions. The legs and wings are translucent white and the eyes are dark brown. The antennae are curved towards the ventral surface and carried loosely over the tips of the wings and the posterior tibiae, extending to the sixth abdominal segment. The front wings are folded ventro-posteriorly, covering the hind wings, and reach to the posterior femora. The prothoracic and mesothoracic legs are folded close to the ventral surface and lie between the tips of the wings and antennae. The palpi lie between the prothoracic tibiae and extend to the first tarsal segment. The posterior tarsi reach almost to the tip of the body, the median tarsi to the sixth abdominal segment and the anterior tarsi to the third abdominal segment.

As with *P. ribesii* the pupal stadium is of short duration, most of the time in the cocoon being spent in the prepupal instar.

The Life-Cycle of P. leucotrochus.

In contrast with *P. ribesii*, *P. leucotrochus* is univoltine. Adults are on the wing during the first week of May, and larvae are fully fed by the end of May or early June. The larvae go to earth in the early part of June and remain in the soil in cocoons until the end of April or early in May in the following year.

Up to the present no example of retarded development, characteristic of *P. ribesii*, has been observed in the case of *P. leucotrochus*, all the specimens reared in captivity having emerged at the normal period.

In view of these observations it is difficult to understand Miss Ormerod's account of her correspondent's observations in Somerset, viz. that *P. leucotrochus* appeared a month or six weeks later than *P. ribesii*. In Gloucestershire the single brood of *P. leucotrochus* synchronised almost exactly with the first brood of *P. ribesii*, from the emergence of the adults from the overwintered larvae to the maturing and cocooning of the larvae (*vide* diagram, p. 15). Where individuals of the first brood of *P. ribesii* were univoltine, their development followed that of *P. leucotrochus* very closely.

P. leucotrochus, like *P. ribesii*, is parthenogenetically arrhenotokous, only mated females producing females.

From a study of *P. leucotrochus* and *P. ribesii*, which closely resemble each other in appearance and development, it seems possible that *P. leucotrochus* was the parent stock, and that multi-voltine strains may have arisen and ultimately developed into the prolific species, *P. ribesii*.

Bionomics of *Pristiphora pallipes*, Lep.

The larvae of *Pteronidea ribesii* are frequently accompanied by the smaller green larvae of another *Ribes*-infesting sawfly, *Pristiphora pallipes*, Lep. This species is fairly common and occasionally abundant in this country, but is more frequently recorded from the Continent, where in Holland and France it causes considerable injury to plantations of gooseberries and red currants.

Though recorded and described by Cameron[1] and Theobald,[9] the most detailed account of the species is that of Chawner & Peacock[2] in 1923. The following account concerns the bionomics as observed under the conditions prevailing in the north-west of England where the species is widely distributed.

Habits of the Adults (Pl. v, fig. 1).

On emergence from the cocoon the female is active, particularly during the early part of the day. In bright sunny weather the insects run about over the leaves, taking short, somewhat awkward flights from leaf to leaf and branch to branch, sometimes stopping to scrape the surface of the leaf with the mouth-parts or to take up drops of moisture from the leaves or tips of the shoots. If the bush is shaken they drop at once to the ground with wings and legs folded close to the body, and remain motionless for a short time before either running over the soil in search of the trunk, which they climb to reach the foliage, or, more rarely, taking flight. During dull weather or in the evenings they rest on the undersurfaces of the leaves or among the petioles of the cluster of leaves at the tips of the shoots. Oviposition may take place within a matter of five minutes after emergence, but this is not surprising since as many as four days may have intervened between the emergence from the pupal membrane and the escape from the cocoon.

Under laboratory conditions eight adults of different generations were found to live 7, 7, 7, 6, 12, 7, 10, 6 days respectively after emergence. Observations under field conditions indicate that the duration of life may be much less than this. In the spring of 1928, on the site of an outbreak of *P. pallipes* in 1927, it was found that adults first emerged on 4th May and were very abundant for two days, but by 7th May scarcely any were to be found except after careful searching. By that time, however, eggs were plentiful.

The ovipositing female walks excitedly over the leaves, with the antennae waving and often bent down in front, and the tip of the abdomen lowered slightly to touch the leaf surface. On encountering the edge of the leaf the body is arched and the cerci at the tip of the abdomen are moved over the tissue. The insect comes to rest

astride the leaf with the tip of the abdomen pressed close against the edge, and the body supported by the legs, the two front pairs extending forwards and the hind pair backwards. The saws are gradually exserted and forced into the leaf edge immediately beneath the lower epidermis. They are at first almost fully extended posteriorly in a line continuous with the dorsum. Then the abdomen is gently arched while the saws work forwards, describing an arc of a circle. When the incision is completed the abdomen remains arched and the egg is passed between the saws into the leaf tissue. When the egg is in position the saws are gradually withdrawn along their original path, leaving the egg firmly held between the lower epidermis and the mesophyll. The whole operation requires from one to just over two minutes, according to the ease with which the tips of the ovipositor engage the leaf tissue. The following lengths of time were noted for the deposition of ten eggs by one female: 1′ 50″, 1′ 45″, 2′ 20″, 1′ 0″, 1′ 10″, 1′ 10″, 1′ 0″, 1′ 50″, 1′ 40″, 1′ 0″, a total of 38 minutes being required for the laying of the ten eggs and the selection of suitable sites.

Although the eggs of *P. pallipes* are usually deposited in the edges of the leaves, they are occasionally placed near the veins, especially when the leaves are young and the veins rather prominent. In such circumstances it seems likely that the veins approximate the leaf edges in thickness and excite a similar response. Of 54 eggs laid by a female, 45 were laid along the edges of the leaves and 9 near the veins.

In order to form some idea of the number of eggs laid by a female, specimens were kept in captivity and the numbers of eggs recorded. Four females laid 54, 24, 13 and 41 eggs respectively, and though this indicates considerable variation in the number, the average of 33 per female agrees with that given by Chawner & Peacock.[2]

Generally the female lays only one egg on a leaf, but where the leaves are large, several eggs may be laid. Occasionally the insect may return and deposit an egg on a leaf which has already received one, or may oviposit on a leaf on which the eggs of other females have been placed.

Observations on the distribution of the eggs of *P. pallipes* out of doors gave the following data:—

Bush 1 ...	4 shoots	... 1 egg on each	
	1 shoot	... 2, 2, 1, eggs on 3 leaves	Total 9 eggs.
Bush 2 ...	3 shoots	... 1 egg each	
	2 shoots	... each with 2 leaves containing 1 egg	Total 7 eggs.
Bush 3 ...	3 shoots	... 1 egg each	
	1 shoot	... 3, 2, 1, eggs on 3 leaves	
	1 shoot	... 3, 1, 1, eggs on 3 leaves	Total 14 eggs.
Bush 4 ...	5 shoots	... 1 egg each	
	1 shoot	... 1, 2, eggs on two leaves	
	1 shoot	... 3 eggs on each of 2 leaves	
	1 shoot	... 3 eggs on one leaf	Total 17 eggs.

These figures indicate the manner in which the eggs of *P. pallipes* are scattered over the bushes, and the tendency of the insects to lay only one egg on a leaf is also apparent. A total of 47 eggs occurred on 23 shoots and of these 24 were laid singly on separate leaves, 2 eggs to a leaf occurred in 4 instances and 3 eggs to a leaf in five instances.

In the laboratory tests were carried out on the effects of leaf character on oviposition. It was noted that "Careless," a variety with fleshy leaves and comparatively little pubescence, was much preferred to "Whinham's Industry,"

a smaller-leaved variety with a considerable quantity of hairs on the edges of the leaves. In the case of "Whinham's Industry" the female was observed to try to make contact with the leaf edge, even partly inserting the saws, and then abandon the attempt. Trials of as many as eight or ten sites were sometimes made before an egg was finally inserted.

The Egg Stage (Pl. i, fig. 4).

The egg of *P. pallipes* is elliptical and approximately 1·1 mm. long and 0·35–0·40 mm. broad. When first laid it is usually completely enclosed by the leaf tissue and the site is only indicated by a slight swelling on the lower surface of the leaf. When dissected from the leaf it is translucent white, but within the leaf tissue it has a distinct pale greenish tint. A few days after oviposition the site of the egg becomes more readily discernible owing to the increase in size which it undergoes within the nidus. This swelling of the egg during development has been thought to be due to the absorption of moisture from the plant tissue with which it is in close physical relationship. Peacock[7] has observed that when a gooseberry shoot bearing eggs of *P. pallipes* is placed in a weak solution of eosin the eggs in their leaf-pockets become stained with red, thus indicating that absorption of moisture from the surrounding tissue can take place. In other experiments he has shown, however, that the eggs of *P. pallipes* develop when merely stuck on the leaf, and concludes that the characteristic swelling is mainly intra-ovum in origin and the deposition of the egg in an egg slit is primarily for protection.

In 7–9 days the outlines of the embryo become discernible, and the eye-spots and tips of the mandibles can be seen through the chorion as small brownish areas. About two days later the mandibles can be seen working spasmodically opening and shutting, and finally the chorion is gripped and an opening effected.

The period of incubation seems to vary between 8 and 11 days, averaging about 10 days, both under laboratory conditions and under normal conditions out of doors.

The Larval Stage (Pl. iv, fig. 3).

At eclosion the larvae vary from 2·0 to 2·2 mm. in length. The body is translucent whitish. The head is dull whitish to smoky with the sutures distinct, and is sparsely covered with short whitish setae, the eye-spots being brown and distinct. The mandibles and antennae are of a brownish colour, the former darkening fairly quickly. The legs, particularly those of the metathorax, are stoutish with light brown tarsal claws. The prothoracic spiracles are distinct and the whole body covered with fine pale setae. The head gradually darkens after eclosion and appears large for the slender, somewhat tapering body. Prolegs occur on segments 5, 6, 7, 8, 9, 10 and 13.

When the eggs are inserted in their usual position, the larvae find themselves on the edge of the leaf immediately on hatching. Larvae hatching from eggs inserted near a vein make their way at once to the leaf edge. At first the larvae wander rather awkwardly along the edges of the leaves, the epidermal hairs appearing exceedingly difficult to circumnavigate. After a short time, however, the mandibles are used to bite the leaf hairs, and ultimately, within twenty-four hours after eclosion, the larvae settle down to feed along the leaf edges in characteristic sawfly fashion.

After feeding has begun the body assumes a greenish tint from the contents of the alimentary canal. The head continues to darken, until by the end of the second day it is quite black and shining. The sclerites of the legs also darken and become more distinct. On the third day feeding is somewhat checked, and the first ecdysis occurs on the third or fourth day. Occasionally at this ecdysis the larvae eat the shed skin and even part of the head-capsule.

In the second stadium feeding is resumed with increased vigour and pellets of frass are thrown out with considerable force. While feeding the larvae rest along the leaf edge with the tip of the body more or less raised off the leaf or slightly curled to one side. In this instar the larva measures about 4 mm. The body retains its pale leaf-green coloration and the head is distinctly black with short stout pale setae. The second stadium lasts three to five days.

After the second moult the shed skin may be partly eaten, but no attempt at devouring the head-capsule has been observed. During the third stadium the larva is pale green with a black head and attains a length of about 6 mm.

About four days later the fourth ecdysis occurs. At this moult the larva assumes a bright green colour quite distinct from the transparent green of the previous instars. The head of the fourth instar larva is mottled with brownish areas on greenish yellow. After this moult only a feeble attempt to eat the sloughed skin is made by some of the larvae, as though the habit was gradually disappearing. The duration of the fourth stadium varies with the time of the year, the summer broods feeding from four to seven days before spinning up and the autumn brood feeding rather longer. When fully fed the larvae of *P. pallipes* attain a length of about 10 mm.

Observations on the duration of larval life in *P. pallipes* are summarised in the following table.

TABLE IV.

Hatched	Duration of stadia in days				Larva in cocoon	Total no. of days
	1st	2nd	3rd	4th		
16.vi.27	—	—	—	—	3.vii.27	17
30.vii.27	—	—	—	—	14.viii.27	15
17.iii.28	4	4	4	7	5.iv.27	19
4.iv.29	5	6	4	4	23.iv.29	19
6.iv.29	5	5	4	4	24.iv.29	18
20.v.29	3	3	2	4	1.vi.29	12

The duration of larval life, from the time of eclosion from the egg to the spinning up of the fully fed larva, seems to vary slightly with the time of the year. The spring and summer broods mature in from 12 to 18 days, but the autumn brood may require as long as three weeks to become fully fed.

Feeding along the edges of the leaves is characteristic of all stages of the larvae of *P. pallipes*. During feeding the larvae exhibit little movement except in the discharge of frass. Though parasites have been observed running about near the feeding larvae, the simultaneous movements to repel the parasites, such as have been described by Cameron and Reh,[8] were not observed. When disturbed the larvae seem to flatten themselves close to the edges of the leaves on which they are feeding, where their inconspicuous coloration partly obscures them. As has been previously noted by Chawner & Peacock (*op. cit.*), where larvae and eggs occur on the same leaf the larvae do not interfere with the eggs but leave a strip of tissue round them which maintains suitable conditions for their development.

When about to undergo ecdysis the larva hangs head downwards supported by the caudal prolegs. The head-capsule splits along the epicranial suture on each side of the frons, and the head is gradually withdrawn and the split capsule passed back along the sides of the body. For some time after the head is withdrawn the capsule remains attached to the buccal cavity pending the complete detachment of the intima of the stomodeum. In the meantime the body is worked forward rhythmically and the old skin gradually pushed backwards until it is held only at the caudal segment. When the head is entirely free the larva obtains a grip on the leaf with the

legs and prolegs and the caudal region is finally withdrawn from the old skin, which remains attached to the leaf stalk. In the insect under observation the time required for ecdysis was about 7 minutes.

Immediately after ecdysis the larva is creamy white except for the eye-spots and the tips of the mandibles, which are brown. In a short time, however, normal coloration is assumed, the head and legs becoming brown and the body green.

The Prepupal Stage (Pl. iv, fig. 4).

In contrast with the larvae of *Pteronidea ribesii* and *P. leucotrochus*, the larvae of *Pristiphora pallipes* do not undergo a larval ecdysis after the cessation of feeding. The fully fed larvae of *P. pallipes* remain about the leaves for some hours after ceasing to feed. During this time the contents of the alimentary canal are voided, and the larvae contract slightly and become a clear bright green. They then proceed to construct cocoons, an operation requiring about a day.

The parchment-like cocoons, which average about 5·8 mm. long and 2·5 mm. wide, are elliptical in shape. At first they are pale straw-coloured, or straw-coloured with a tinge of green, but gradually become light brown and then dark brown with age. In making the cocoon the larva first spins coarse strands to give the cocoon its general shape, then finer strands are added to make a close mesh, and the cocoon is rendered translucent and finally opaque by the addition of saliva.

The summer broods of larvae make their cocoons about the bushes, either in folds or curls of leaves, beneath dead or dying leaves, near the branches or trunk, or under dead leaves which may be attached to clods. The larvae of the autumn brood, however, usually enter the soil to a depth of about half an inch and spin up in suitable crevices on the side of lumps of soil.

The Pupal Stage (Pl. iv, fig. 2; v, fig. 3).

Within the cocoon the larva turns round and round more or less continuously, gradually contracting and the folds of the integument becoming more pronounced. In the case of the spring and summer broods the final larval skin is shed about eight days after the construction of the cocoon, and the delicate whitish pupa is revealed. In the course of a further two or three days the pupa gradually darkens and the form of the adult becomes distinct.

The pupa is about 6 mm. in length. The prothoracic and mesothoracic pairs of legs are folded beneath the body, the prothoracic legs reaching to the metathoracic coxae and the mesothoracic legs to the third abdominal segment. The metathoracic legs lie along the sides of the body, the tibiae and some of the tarsal segments being closely applied to the flanks, while the extreme tarsal segments are free. The forewings are curved towards the ventral surface of the body, the tips reaching to the tips of the prothoracic tibiae, and overlying the tips of the hind wings. The antennae lie along the sides of the body on the outside of the wings, and reach to the posterior edge of the first abdominal segment. The head is bent forwards and downwards so that the palpi lie on the first pair of coxae.

The period spent in the cocoon varies from 14 to 16 days in the early broods, but the autumn brood spends the winter in the cocoon (about 220 days). The adult escapes from the cocoon through a circular opening which is cut in one end.

Parthenogenesis.

In contrast with the females of *Pteronidea ribesii* and *P. leucotrochus*, which are parthenogenetically arrhenotokous or male-producing, the females of *Pristiphora pallipes* are thelytokous or female-producing. The species appears to depend mainly on parthenogenesis for its survival, although males have occasionally been recorded.

During the past four seasons the writer has reared and collected some hundreds of specimens of *P. pallipes*, but so far has not secured a male either under laboratory conditions or under the natural conditions prevailing in the field.

The Annual Cycle of Generations.

Adults of *P. pallipes* emerge from overwintered larvae towards the end of April and the beginning of May. These oviposit immediately and the first brood of larvae hatches about ten days later. The larvae mature in 18–19 days and some may spin up before the end of May.

Since the emergence of adults from overwintered larvae extends over some days and egg-laying may continue for about a week, adults from the first brood of larvae have a scattered emergence during June. As a result of this the succeeding broods are not clearly defined, and from June until September eggs and larvae may be found about the bushes. Careful field observations and breeding experiments with insects in captivity show that there are normally four generations during the season, and the retarded development characteristic of *Pteronidea ribesii* has not been

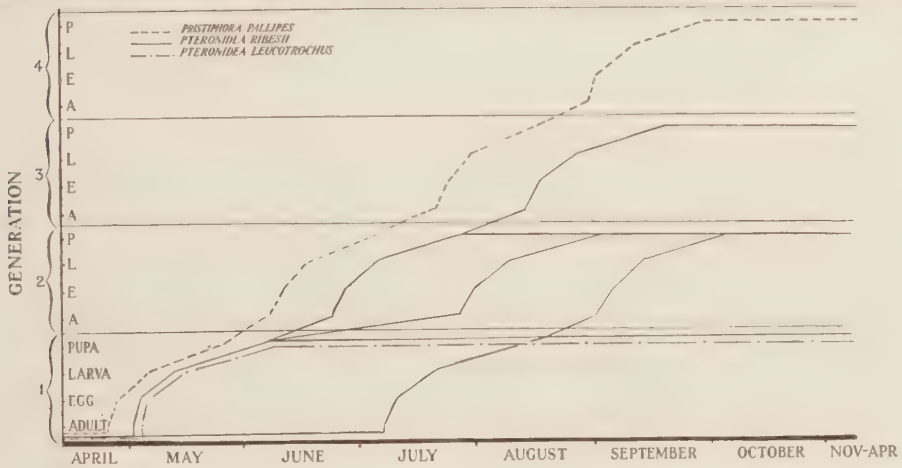


Diagram showing the annual cycle of generations in *Ribes*-infesting sawflies.

observed in *P. pallipes*. Since practically all the adults of *P. pallipes* are females capable of parthenogenetic reproduction, an outbreak of this insect may develop speedily.

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Fig. 1. *Pteronidea ribesii*, ♂.



Fig. 2. *Pteronidea ribesii*, ♀.



Fig. 3. *Pteronidea ribesii*, ovipositing.



Fig. 4. Eggs of *P. ribesii* and *Pristiphora pallipes*; the former along veins; the latter in marginal incisions.

Stages of Pteronidea ribesii and Pristiphora pallipes.



Fig. 1. *P. ribesii*, larvae in final instar.



Fig. 2. *P. ribesii*, pre-pupal instar extracted from cocoon.



Fig. 3. *P. ribesii*, pupa in cocoon.



Fig. 4. *P. ribesii*, cocoons as taken from soil.

Stages of Pteronidea ribesii.



Fig. 1. *P. leucotrochus*, ♀.



Fig. 2. *P. leucotrochus*, eggs.



Fig. 3. *P. leucotrochus*, larva in final instar.

Stages of Pteronidea leucotrochus.



Fig. 1. *P. pallipes*, ♀.

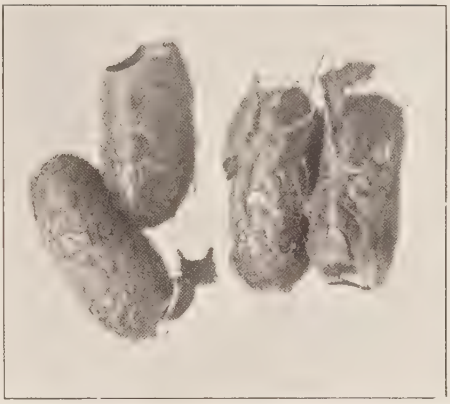


Fig. 2. *P. pallipes*, cocoons.



Fig. 3. *P. pallipes*, larva in final instar.



Fig. 4. *P. pallipes*, mature larva prior to cocooning.

Stages of Pristiphora pallipes.



Fig. 1. *P. pallipes*, testing leaf surface prior to ovipositing.



Fig. 2. *P. pallipes*, cocoons on defoliated shoot of gooseberry.

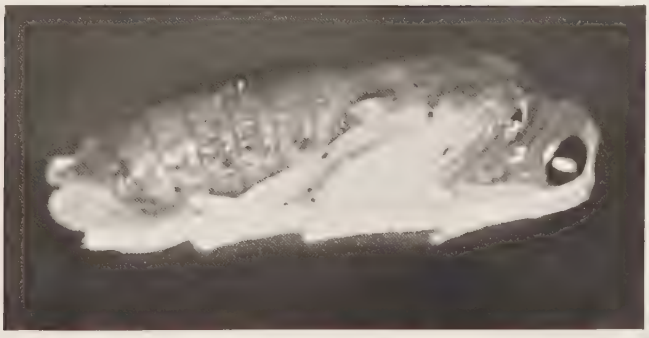


Fig. 3. *P. pallipes*, pupa extracted from cocoon

Stages of Pristiphora pallipes.

ON THE STRUCTURE OF THE BUCCAL CAVITY, PHARYNX AND SPERMATHECA IN SOUTH AMERICAN *PHLEBOTOMUS*.

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(Plate VI.)

Through the kindness of Prof. Mazza, Buenos Aires, Dr. P. A. Buxton, of the London School of Tropical Medicine, and Prof. Brumpt, Paris, I have had the opportunity of examining a collection of sandflies from South America. It appears that, as in the sandflies of the Old World, the structure of the buccal cavity and spermatheca, and to a smaller degree that of the pharynx, affords an easy mean of distinguishing the five species at my disposal.

The buccal cavity in the South American species dissected has a rather complex structure of a type common to all the five species examined. It is rather difficult to form an opinion as to its structure from the dorsal aspect, but a sagittal section shows that the fundamental form is the same as in the sandflies of the Old World (fig. 1). The buccal cavity consists of a ventral plate and two dorsal ones, which unite posteriorly to form a single thick pigmented plate. This so-called pigmented area often seems to have a long anterior projection, which is really the median suture of the two dorsal plates. Posteriorly the dorsal plate curves downwards and backwards, then bending forwards again forms the pigmented thickened area to which

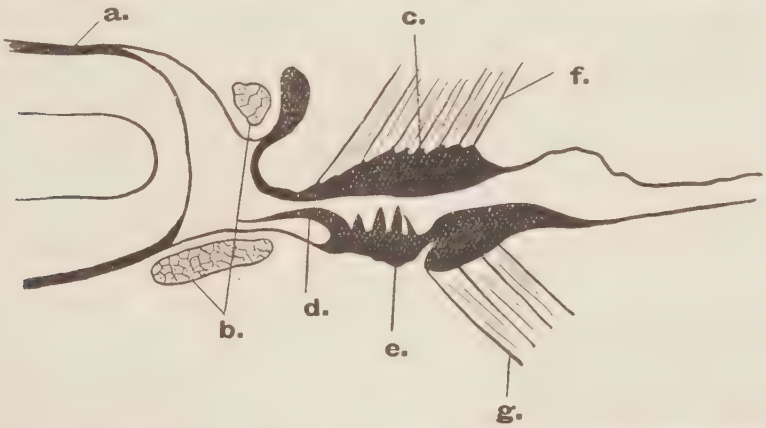


Fig. 1. Sagittal section through buccal cavity of female of *Phlebotomus intermedius*, L. & N.: *a*, anterior end of pharynx; *b*, sphincter muscle; *c*, pigmented area; *d*, horizontal row of teeth; *e*, vertical teeth; *f*, posterior clypeal muscles; *g*, salivary muscle.

the posterior clypeal muscles are attached. It apparently acts as a spring, closing the buccal cavity when the clypeal muscles are relaxed. The ventral plate of the buccal cavity bears at its posterior margin two systems of teeth, one of several rows of vertical short stumpy teeth and a row of very long pointed teeth, rather widely separated, arising from the posterior margin and projecting horizontally into the lumen of the connective tube. In the dorsal aspect the curvature of the dorsal plate shows itself as a curved line behind the horizontal teeth, which appear in optical

section to lie inside it but which really lie underneath. The armature of the pharynx is rather weakly developed and consists of ridges and blunt teeth in the posterior part.

In the male the armature of the buccal cavity and pharynx is much less developed but is apparently of the same type as in the female, at least in some species.

The spermathecae differ widely in various species and although there are many common characters in the five species examined, *e.g.*, in the structure of the buccal cavity and the male genitalia, there is no resemblance in the spermatheca except in two species which are also nearly related in other characters. As pointed out already elsewhere the structure of the spermatheca is apparently a specific character, while the structure of the buccal cavity and the male genitalia are of higher systematic rank.

The species dealt with in this paper have four big spines on the distal segment of the superior clasper of the male genitalia. In some species (*e.g. P. migonei*) there is a small fifth spine arising near the terminal spine. This little spine is similar to the small anterior spine on the corresponding segment in the *minutus* group of the Old World *Phlebotomus*.

Phlebotomus intermedius, Lutz & Neiva (1912).

Syn. *P. mazzai*, Patterson & Shannon (1926).
P. neivai, Pinto (1926).

During the preparation of this paper Nitzulescu has published a full description of the female of this species, giving drawings and measurements of all the important

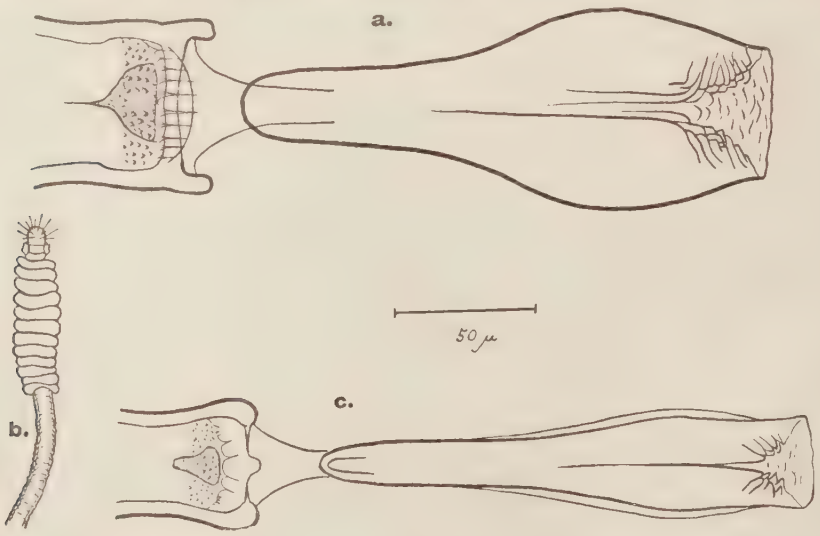


Fig. 2. *P. intermedius* : *a*, buccal cavity and pharynx of female ; *b*, spermatheca ; *c*, buccal cavity and pharynx of male.

characters. The present description is therefore confined to parts necessary for comparison with the other species dealt with in this paper.

♀ Palp formula : 1, 4, 2, 5, 3. Relative lengths of segments : 1, 4, 4, 1·3, 3. Antennae : segment 3 > 4+5.

Buccal cavity (text-fig. 2, *a* ; pl. vi, fig. 2) with the vertical group of teeth on the ventral plate consisting of several irregular rows of well-marked short conical teeth ; the horizontal row with about 10–12 very long pointed teeth set in regular intervals ; the pigmented area is roughly triangular, with deep corrugations. Pharynx twice as broad posteriorly as anteriorly, with weakly developed teeth and ridges. Spermathecae (fig. 2, *b*) similar to those of *P. papatasii*, consisting of about 10–13 segments with narrow ducts which unite shortly before their exit ; the apical knob bearing the fine ducts that lead into the gland cells rather large, sometimes double (Nitzulescu).

♂. The buccal armature (fig. 2, *c*) resembles that of the female, but is so weakly developed that it has to be dissected out to make out its finer details. There are many small vertical teeth and 4–5 long horizontal ones ; the pigmented area a narrow triangle with its base posteriorly ; pharynx very narrow, almost parallel-

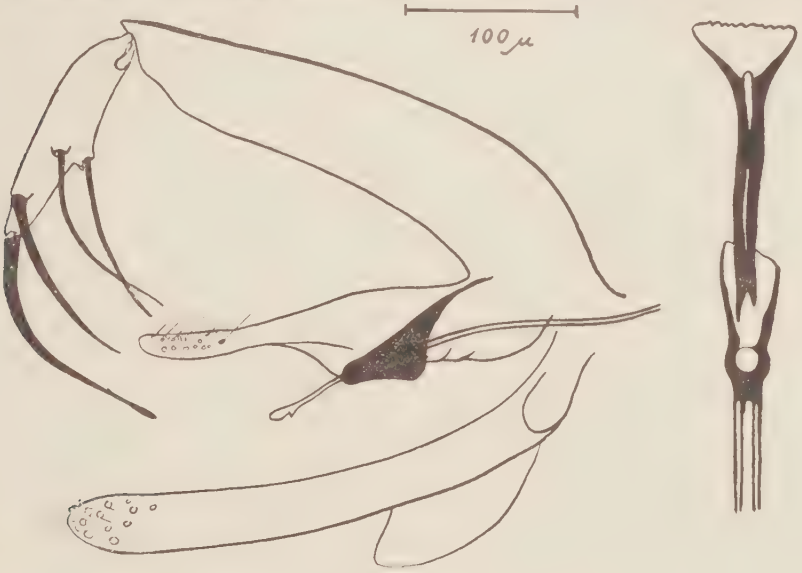


Fig. 3. *P. intermedius :* male genitalia.

sided, with a few ridges in its posterior part (fig. 2, *c*). Genitalia (fig. 3) : the apical segment of the superior clasper with four spines, the terminal one being the thickest and longest ; the three others, of which two are situated at about the middle of the segment and one at about the junction of the third and apical quarters, are of about the same length, the last mentioned one being thicker than the two others ; no fifth accessory spine ; the intermediate appendages straight and simple, bearing a few short hairs on the dorsal surface ; penis short and conical ; genital pump very large, with wide filaments, whose endings are flattened and widened elliptically.

Argentina : 34 ♀♀, 7♂♂, San Pedro, Jujui (*Mazza*) ; 5 ♀♀, Tabacal (*Mazza*). Brazil : 1 ♂, Rio de Janeiro (*Beaurepaire Aragão*) ; 4 ♀♀, Rio de Janeiro (*Brumpt*).

Phlebotomus migonei, França (1921).

♀. Palp formula : 1, 2, 4, 3, 5. Relative lengths of segments : 1, 3, 3·6, 3·3, 7. Antennae : 3≷4+5.

Buccal cavity (fig. 4, *a*) with the vertical group of teeth consisting of a single row of about 10 short stumpy teeth ; four large pointed horizontal teeth distributed in

equal intervals over the whole breadth of the buccal cavity ; pigmented area very faint, carrot-shaped. Pharynx with a number of blunt teeth and ridges in the posterior part, which is about twice as wide as the anterior part. Spermathecae

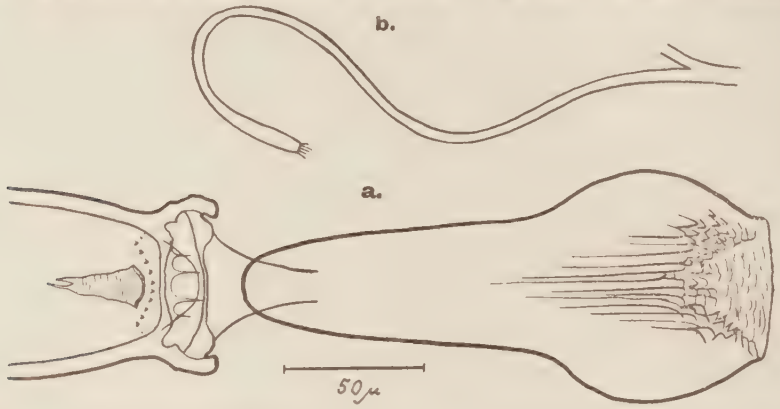


Fig. 4. *Phlebotomus migonei*, França : *a*, buccal cavity and pharynx of female ; *b*, spermatheca.

(fig. 4, *b*) with practically no capsule, nor widening at all at the end, being simply two very long smooth ducts with a few short " hairs " at the end ; they unite at a very short distance before their common opening.

♂. Palps and antennae as in female. Buccal cavity with the armature much reduced and consisting of a few small irregularly distributed teeth ; no pigmented

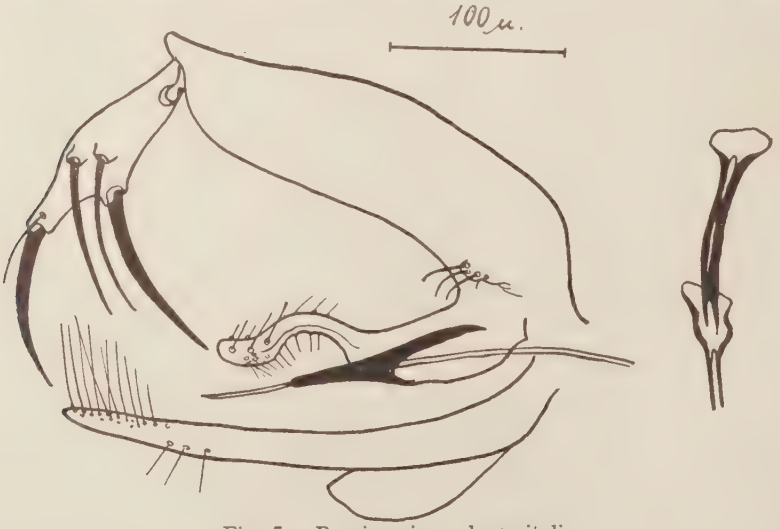


Fig. 5. *P. migonei* : male genitalia.

area. Genitalia (fig. 5) with the distal segment slightly less than half the proximal one, bearing four large spines and a small accessory spine arising near the base of the terminal one, which latter is shorter than the segment and very thick ; another spine of the same thickness and slightly longer at about the middle of the segment and two thinner ones more proximally ; a small tubercle bearing a few short hairs at the inside of the proximal segment near its base and near the ventral surface ;

median appendage with a long curved neck : penis slender and conical, and the genital filaments fine and long, ending in a point ; inferior claspers pointed and as long as the basal segment of the superior clasper.

Dyar in his paper on American *Phlebotomus* considers *P. araozi* to be a synonym of *P. migonei*. The palp formula of these two species, however, is quite different and so is the arrangement of the spines on the distal segment of the superior clasper in the male genitalia. The species described by Mazza from Tabacal corresponds in every respect with *P. migonei* according to França's description.

ARGENTINA : 20 ♀♀, 3 ♂♂, San Pedro, Jujui (*Mazza*) ; 11 ♀♀, 46 ♂♂, Tabacal (*Mazza*).

Phlebotomus cortelezzii, Brèthes.

♀. Palp formula : 1, 4, 2, 3, 5. Relative lengths of segments : 1, 3·6, 4, 2·5, 7. Antennae : 3≧4+5.

Head markedly longer than broad, length to breadth=1·5 : 1·3 (Pl. vi, fig. 1)· Buccal cavity (text-fig. 6, *a*) with four large horizontal teeth set rather near each other in the median third ; in front of each horizontal tooth a small vertical one ;

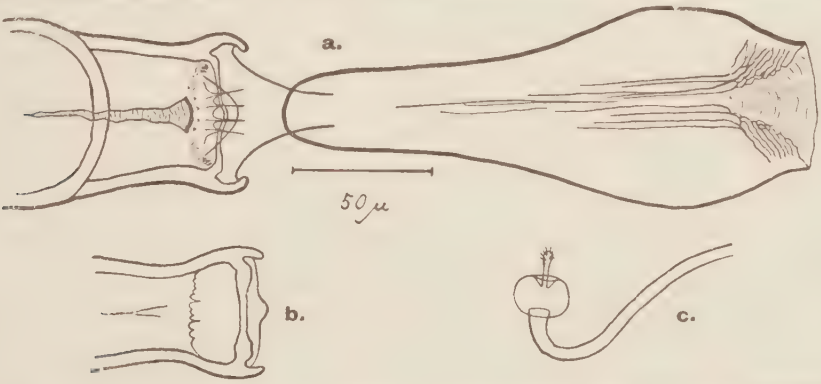


Fig. 6. *Phlebotomus cortelezzii*, Brèthes : *a*, buccal cavity and pharynx of female ; *b*, buccal cavity of male ; *c*, spermatheca.

two lateral groups of very small vertical teeth arranged in oblique elongated patches ; the pigmented area very faint and elongated. Pharynx three times as broad posteriorly as anteriorly with some faint ridges in the posterior portion. Spermathecae (fig. 6, *c*) spherical capsules with a knob on a long pedicle, ducts narrow and smooth.

♂. Palps, antennae and head as in ♀. Buccal cavity (fig. 6, *b*) much reduced, only a few small pointed irregularly situated teeth present. Genitalia (fig. 7) with distal segment of superior clasper more than half length of proximal one, rather elongated and conical, with four big spines : a very thick terminal one, a thinner one at middle of the segment, and two still smaller ones at the proximal third ; a small accessory spine near the base of the terminal one ; near the base of the proximal segment, at the inner surface ventrally, a tubercle situated in a circumscript area, which bears three very long hairs and several short ones. Median appendage with a slender neck, a thickened rounded head and a ventral pointed projection near the apex, and bearing dorsally about 10–12 stout vertical hairs ; penis short, conical and pointed ; genital pump rather large but smaller than that of *P. intermedius* ; filaments pointed ; inferior claspers markedly longer than the proximal segment of

the superior clasper, pointed and bearing a number of long thin hairs on the dorsal surface.

ARGENTINA : 2 ♀♀, San Pedro, Jujui (*Mazza*) ; 4 ♂♂, 4 ♀♀, La Plata (*Brèthes*).

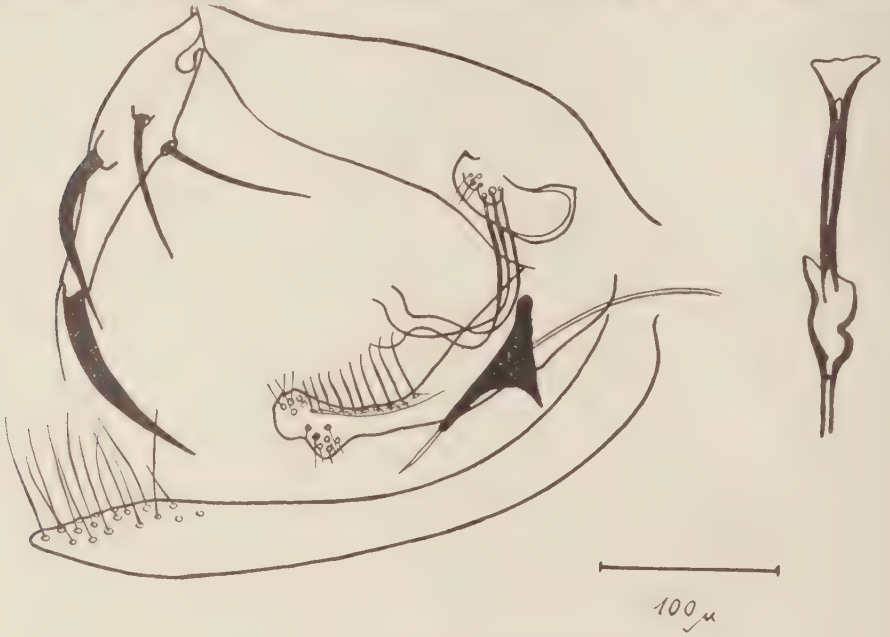


Fig. 7. *P. cortelezzii :* male genitalia.

Phlebotomus ? trinidadensis, Newstead (1922).

♀. Palp formula : 1, 4, 2, 3, 5. Relative lengths of segments : 1, 3·6, 4·4, 3·3, 8. Antennae : 3 > 4 + 5.

Head slightly longer than broad, length to breadth = 1·2 : 1·1. Buccal cavity (fig. 8, *c*) very similar to that of *P. migonei* ; four large pointed horizontal teeth and

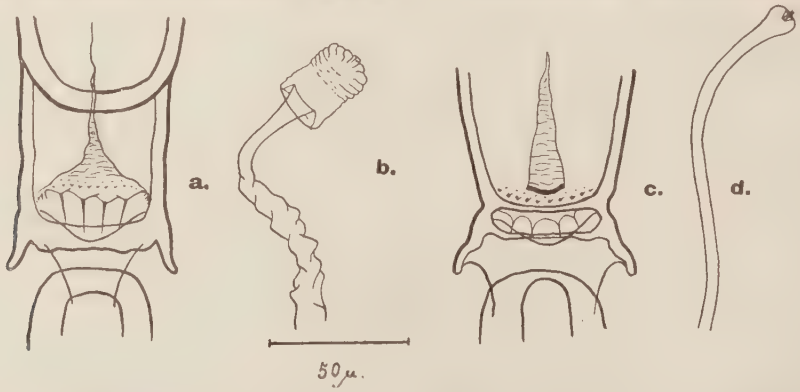


Fig. 8. *Phlebotomus* sp. : *a*, buccal cavity of female ; *b*, spermatheca. *P. ? trinidadensis*, Newst. : *c*, buccal cavity of female ; *d*, spermatheca.

one row of small vertical ones ; pigmented area very faint. Spermathecae (fig. 8, *d*) long thin tubes with a very small rounded head.

This species resembles closely *P. migonei*, from which it can be distinguished by the spermatheca, the palp formula and minor details in the buccal cavity. Dyar considered this species as identical with *P. cruciatus* because of the similar palp formula; but this formula is present in several species, so that a more exact comparison is needed before the identity or difference of these two species can be established.

Whether the specimens examined are really *P. trinidadensis* or belong to another species recorded from Trinidad I cannot decide, as I had no males at my disposal.

TRINIDAD: 7 ♀♀ (*K. S. Wise*).

Phlebotomus sp.

Among several specimens of *P. intermedius* received from Prof. Brumpt there was one female which differs from the other species described above in several characters. It is impossible with the material at my disposal to decide whether it belongs to an insufficiently described or to a new species.

Palp formula: 1, 4, (2, 3), 5. Relative lengths of segments: 1, 3·9, 4, 2·3, 7·6. Antennae lacking.

Buccal cavity (fig. 8, *a*) with four long, needle-like, horizontal teeth on broad bases; 2–3 rows of small vertical teeth; pigmented area faint, triangular, with apex anteriorly. Spermathecae (fig. 8, *b*) roughly barrel-shaped capsules with thin walls, the anterior rounded portion having irregular corrugations and ridges; ducts moderately wide and crinkled.

The spermathecae and palps resemble somewhat those of *P. verrucarum* as figured by Shannon.

BRAZIL: 1 ♀, Rio de Janeiro (*Brumpt*).

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METHODS OF REARING AND MAINTAINING LARGE STOCKS OF FLEAS AND MOSQUITOS FOR EXPERIMENTAL PURPOSES.

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London School of Hygiene & Tropical Medicine.

It is essential, when experiments relating to the bionomics of insects are projected, that an adequate supply of material be available at all times; it is also important that the methods employed should not be such as to form too great a proportion of the work. The experiments themselves are the main objective; the technique which ensures the maintenance of a continuous stock of material is subsidiary, and therefore should be so devised as to achieve its object with a minimum of effort and the least expenditure of time. In short, the preparatory work should be as nearly automatic and self-supporting as possible.

Any peculiarities in the behaviour of the insects ought to receive particular attention and not be regarded as of no consequence; attention to even apparently insignificant trifles may mean all the difference between success and failure. Preferences and aversions, unaccountable as they may be, should be utilised by those wishing to rear and maintain large stocks of living insects.

Method of Rearing Fleas.

The methods herein described for the breeding of fleas are successfully employed in the Department of Entomology at the London School of Hygiene and Tropical Medicine. They have evolved mainly from a study of the classical researches conducted by Bacot (1914) in England and Hirst (1926) in Ceylon.

It has been found possible to employ these methods for three species:— *Xenopsylla cheopis*, Roths., *X. astia*, Roths., and *Ceratophyllus fasciatus*, Bosc; at Birmingham, Miss E. K. Sikes has found the plan works equally well with *Ceratophyllus wickhami*, Baker.

Preparing the Breeding Chamber (fig. 1).

The fleas are kept in glass sweet-jars nine inches high and five inches square, in each of which is a clean healthy mouse. Each jar is first of all scrupulously cleaned so as to afford no foothold on the sides to the adult fleas. A layer of fine sifted sand (A) is put in, covering the bottom to a depth of about a quarter of an inch; a pinch of finely ground dried ox-liver is added, which helps in the production of large numbers of fleas, though no comparison has been made with dried blood or blood-soaked rag which formed the chief food for the larvae in Bacot's experiments. A small quantity of oats is then put in for the mouse (B). The oats are autoclaved before use to destroy any mites which may be present, otherwise the latter breed in such enormous numbers that they become a pest. It may also be that certain species definitely attack the flea pupae, though Webster (1930) found that the species infesting his breeding jars in Bombay did not interfere with the output of young fleas. A teaspoonful of oats is added daily, this being sufficient for the mouse; more should not be used, as it merely fills the jar and increases the possibility of fleas escaping when the cover is removed.

For the supply of drinking water the following simple arrangement is used. The end of a short piece of glass tubing of approximately one-fifth of an inch internal diameter is rounded off in a Bunsen flame so that the aperture is reduced to something under half its original size. This is inserted into the bored cork, or preferably the rubber bung, of a specimen tube about three inches long and one inch wide. The glass tubing is so arranged that the wide end is flush with the inside of the bung and the remainder projects externally about an inch and a half. After filling the specimen tube with water and fitting the bung, the whole is suspended upside-down inside the breeding jar by wire attached to the rim (C) ; the mouse drinks by sucking at the narrowed opening of the glass tubing. Two points may be mentioned : firstly, a rubber bung is preferable because if cork is used the mouse gnaws at it and renders

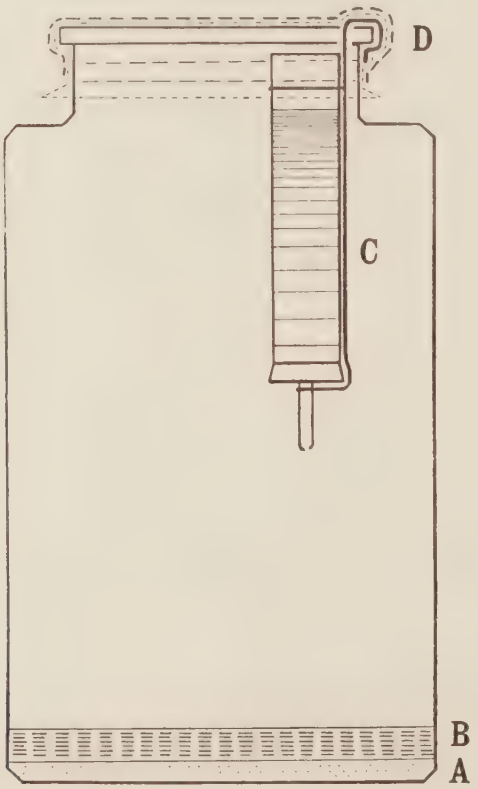


Fig. 1. Flea breeding-jar prepared for reception of mouse and fleas : *a*, sand ; *b*, oats ; *c*, tube containing drinking water suspended by wire ; *d*, covers of voile and perforated zinc.

it useless ; secondly, the glass tubing is simply rounded off in the flame, and not drawn to a point, in order to avoid the formation of air locks which would prevent the mouse from obtaining water.

The jar containing the mouse, its food and drink, and adult fleas of a particular species, is then covered with fine muslin or voile secured by adhesive tape to prevent the fleas from escaping, and a second cap of perforated zinc is fitted over the voile so that the mouse also may not escape (D). It is most important, particularly when more than one species of flea is being cultivated, to use perforated metal caps ,

otherwise, an escaped mouse might enter another jar containing fleas of a different species, in which case the material involved would have to be abandoned.

The breeding jars containing *Ceratophyllus fasciatus* are kept at room temperature, while those containing the species of *Xenopsylla* are kept at 23° C. (74° F.) in a moist incubator; accurate control of humidity is found to be unnecessary.

Collecting adult Fleas.

After a fortnight or three weeks, a second generation of fleas is nearly mature. The covers and drinking tube are removed from the jar, the mouse is transferred with forceps to a convenient vessel, and the rubbish is tipped into another container. The breeding jar is thoroughly cleaned and prepared as before, and the animal returned to it, the covers being left off for a while. A portion of the debris is next put into one side of a large glass battery jar, the opposite side of which is shaded (fig. 2).

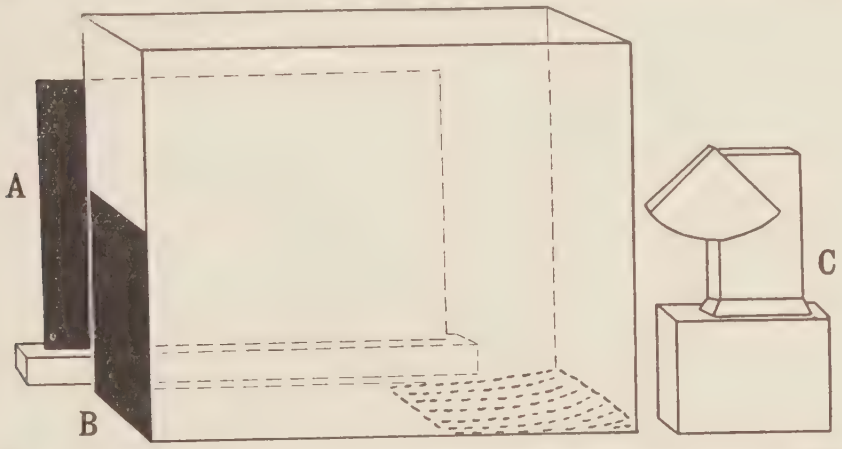


Fig. 2. Battery jar containing debris from which fleas are collected: *a*, black wooden screen at back of jar; *b*, black paper gummed to side of jar; *c*, lamp. The fleas leap away from the light and are collected from the shaded side of the jar.

The jar stands on white paper and the fleas are easily seen leaping away from the light into the shaded portion, from where they are collected; an illustration of the apparatus used for this purpose is shown in fig. 3. The collecting tube (B) is five inches deep and one and a quarter inches wide. The voile cap at (C) must be cleaned occasionally, as it becomes clogged with dust. The opening (E) is reduced from its original diameter so as to avoid taking in large particles of rubbish. After turning on the water-tap the end of the long glass tubing is applied to the fleas, which are drawn up and trapped in the deep specimen tube.

Maintaining the Supply.

When the debris has been cleared of adult fleas, it is dropped into another jar and a second portion treated in the same manner; this process is repeated until the whole mass has been dealt with. The collected fleas are then returned to the mouse, the jar closed and put away. The material thus cleared still contains numerous eggs and larvae; it may be left until required, or examined regularly and the newly emerged adults removed and transferred to the mouse. In any case best results are secured by keeping the debris in a moist atmosphere. The jars are placed on a

galvanised iron wire grid which stands in about two inches of water inside a large battery jar fitted with an air-tight lid. To obtain atmospheres of relative humidities below saturation, appropriate mixtures of sulphuric acid and water are used (Buxton 1931) together with a stand of glass or other acid-proof substance instead of one of metal.

Obtaining unfed Fleas of known Age.

For experiments concerned with the longevity of fleas, it is necessary that freshly emerged adults be employed; to obtain unfed fleas under twenty-four hours old, all that is required is that the debris be sorted in the battery jar and *all* adult fleas removed at least once a day. Or, alternatively, the rubbish is placed in a shallow glass container, such as a petri dish, suspended by wire in a deep glass jar; emerging

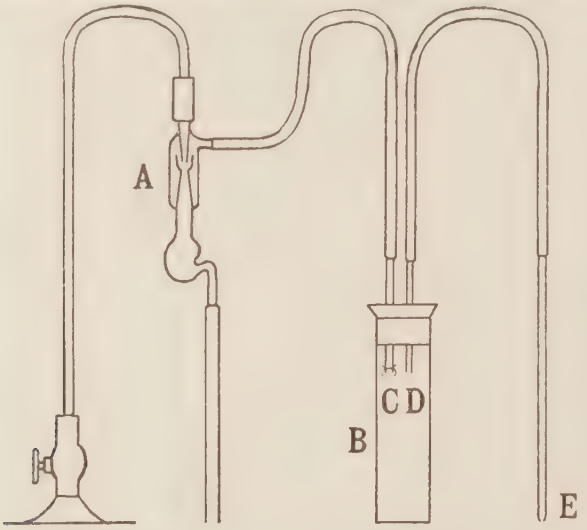


Fig. 3. Apparatus for collecting fleas: *a*, suction-pump attached to water-tap; *b*, specimen tube in which fleas collect; *c*, end of tubing protected by cap of voile; *d*, tubing through which fleas arrive in specimen tube; *e*, fine opening of glass tubing through which fleas are collected.

fleas hop away from the debris and drop into the bottom of the jar, from where they may be collected daily; this gives the same result but on a much smaller scale. An advantage of the first method is that the disturbance of the rubbish through being tipped into the battery jar is undoubtedly a contributory factor in causing the adults to emerge from the cocoon (Bacot 1914); another is that as larger quantities are being dealt with, the period necessary to complete any one series of investigations is correspondingly reduced.

Collecting Larvae.

For the collection of larvae the material is first cleared of all adult fleas in the manner already described; then it is sifted a little at a time through a cylinder of perforated zinc suspended in a deep glass jar. A gentle shake or two causes the fine dust and larvae to pass through, while the larger portions are retained. The sifted dust is then tipped into the large battery jar, spread out in a thin layer over the bottom, and the larvae collected by the suction-pump. The tubing is applied over the larvae without touching so that dust and sand are not collected in too great a quantity.

Collecting Eggs.

To obtain eggs of the fleas, a portion of the material in the breeding jar is dropped into the unshaded end of the battery jar; among the fleas which leap away the pregnant ones are easily distinguishable. These are collected singly and transferred to small tubes into each of which has been put a square of black cloth. The tubes are capped with voile and adhesive tape, put away and occasionally examined during the next two or three days; the eggs are seen against the pieces of black cloth as small glistening white objects and may be moved with a moistened camel-hair brush.

Method of Rearing Mosquitos.

Numerous authors have described methods of mosquito rearing which have satisfied their own particular needs; in some cases, in fact, the breeding has been in the nature of an experiment itself, but for continuous breeding round and round the life-cycle, providing an indefinite number of mosquitos for any experiment, it has been found that a cage must be used which contains everything necessary for the insects' existence. Such a cage has been designed for the rearing of *Aëdes argenteus*, Poir.

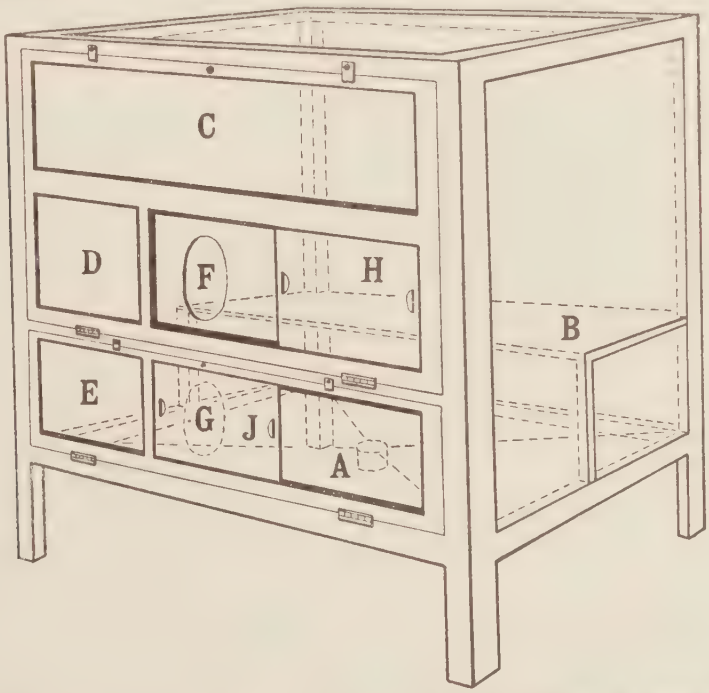


Fig. 4. Mosquito breeding-cage: *a*, circular opening in sloping floor; *b*, shelf for water-tank and fruit; *c*, *d*, *e*, observation windows; *f*, *g*, armholes (*g* shown closed); *h*, *j*, sliding shutters for closing armholes.

The Cage (fig. 4).

The construction of the cage is of special interest; it has a rectangular framework of wood approximately two feet in each direction with the uprights extended below to form legs at the corners. The bottom of the cage is of metal, sloping to a central two-inch circular opening, which is flanged to take a rubber bung (A). In this portion

lives a guinea-pig, from which the female mosquitos obtain their blood-meals. The sloping floor and the bung-hole facilitate cleaning and the removal of litter ; the rubbish can be swept out through the opening in the floor without setting free any mosquitos. In cages with trays which have to be taken out for cleaning, it is practically impossible to prevent mosquitos from escaping by the space through which the tray is withdrawn. At the back is a shelf (B) nine inches from the floor and about ten inches wide which extends across the cage from side to side ; on this is placed a tank holding the breeding water and a dish containing scraps of fruit for the males. The two sides and back of the cage are of wire gauze and the top is of glass, while the whole of the front consists of two doors opening downwards, the lower being only half the depth of the upper. In the top half of the upper door is a fixed glass panel (C) forming an observation window. The lower door and the lower half of the upper door are identical in construction ; the left third of each consists of a fixed glass observation window (D and E), the other two-thirds are of wood. In the left halves of the wooden portion are armholes (F and G) which are closed by wooden slides (H and J) running in grooves and provided with thumb-nail notches. Through the armholes the guinea-pig may be fed and mosquitos collected. The animal may be removed or replaced by opening the lower door, the tank by opening the upper door.

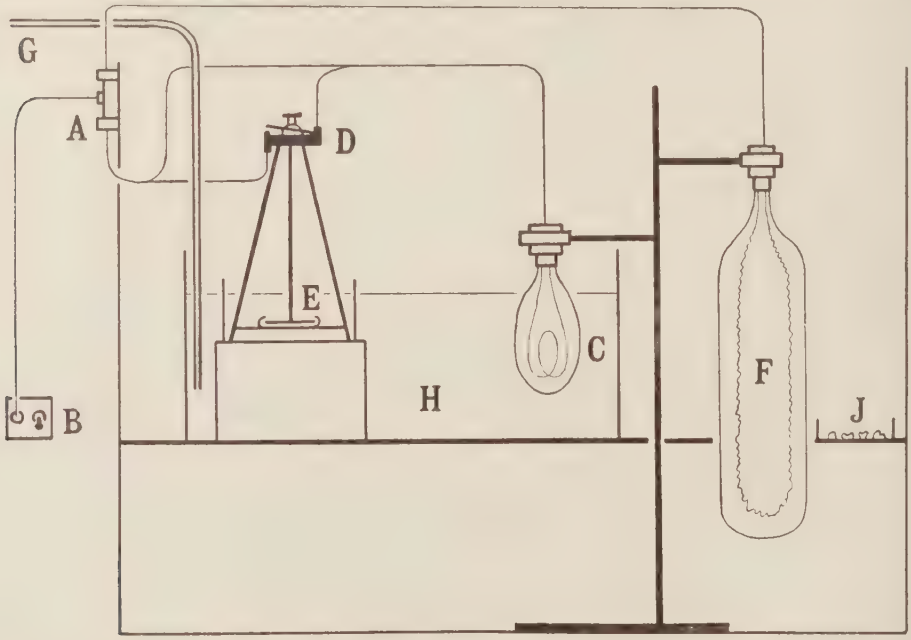


Fig. 5. Apparatus for controlling temperatures of water and atmosphere in mosquito breeding cage : *a*, two-way plug ; *b*, wall switch ; *c*, carbon-filament lamp for heating water ; *d*, make-and-break switch ; *e*, capsule ; *f*, lamp for warming atmosphere ; *g*, tube from tap for replenishing water in tank ; *h*, tank containing water for young stages ; *j*, fruit for males.

Temperature Control (fig. 5).

The temperature of the water is regulated automatically. On the outside of the cage is fixed a two-way plug (A) which can be connected to any convenient electricity supply point (B). The wire from one plug leads to a carbon-filament lamp (C) immersed in the water ; this circuit is intercepted by a make-and-break switch

(D) mounted on an ebonite block, supported on a tripod standing in the tank. Through the centre of the block passes a bone rod, the end of which rests on a submerged capsule (E). When the desired temperature is reached, the expanding capsule pushes up the rod and causes a break in the circuit so that the heat is cut off. Alternately, when the temperature falls, the capsule contracts, allowing the rod to descend so that the metal contact bridges the gap between the studs of the switch ; the circuit is thus completed and the lamp lights up. The other plug on the side of the cage is connected directly to a heating lamp (F) suspended in the cage. At night-time or when the cage is in a cold room, this lamp may be used to warm the atmosphere inside the cage.

Water Supply.

Finally a length of rubber-tubing (G) is connected to a water tap so that water can be added to the tank as required.

The only attention necessary is the daily supply of food for the guinea-pig, the removal of the excrement, bedding and other litter, and the renewal of the fruit for the male mosquitos. The supply of insects is maintained indefinitely.

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Fig. 1. Head of female of *P. cortelezzi* 1851.



Fig. 2. Buccal cavity of female of *P. intermedius* (× 400)

Détails of female Phlebotomus.

THE BIOLOGY OF *ERYTHRONEURA (ZYGINA) PALLIDIFRONS*, EDWARDS.

By Elsie I. MacGill, M.Sc.,

University of Manchester.

Introduction.

The association between insects and virus diseases of plants and the suspicion which at present rests on Jassidae, amongst others, may result in members of this family becoming of increased importance as potential vectors of virus diseases of crop plants. In America leaf-hoppers are already serious pests of cereals and of grape-vines[7, 8, 9, 12, 13, 16, 17], and in the cotton-growing area of Central and South Africa a Jassid forms one of the most important obstacles to the successful cultivation

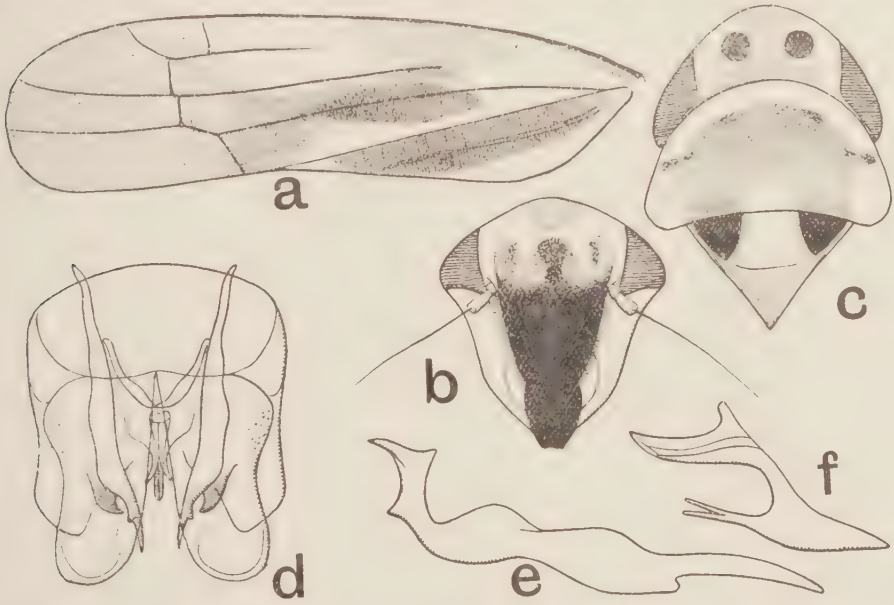


Fig. 1. *Erythroneura parvula*, Boh. (Austria): *a*, tegmen; *b*, face; *c*, dorsal view of head and thorax; *d*, male pygopher in ventral view; *e*, lateral view of paramere; *f*, lateral view of aedeagus. (*a*, *b*, *c*, are from ♀ specimen; *d*, *e*, *f*, are from balsam preparation.)

of this crop[4, 5, 6], so that in these countries a considerable amount of attention has been demanded by this group of insects. In this country, however, the leaf-hoppers have only been regarded as of minor importance, though in recent years increasing interest has been taken in certain species infesting potatoes and glass-house crops[10, 11, 15, 18]. It was suggested to the writer that further knowledge of the biology of these insects was desirable, especially in view of the extreme importance of a nearly related species in many of the African cotton-growing areas, and it was accordingly decided to use the common species infesting glass-houses as a type for investigation with cotton as the food-plant.

It was supposed that the majority of the leaf-hoppers infesting glass-houses belonged to two species, *Erythroneura* (*Zygina*) *parvula*, Boh., and *E. pallidifrons*, Edwards, both of which have been recorded in the open and are therefore supposed to be indigenous to the British Isles, but although the material was collected from several widely separated localities, only *E. pallidifrons* was obtained, so that it seems probable that most of the damage attributed to *E. parvula* is really caused by *E. pallidifrons*. Mr. W. E. China, of the British Museum, states that there is no authentic British male specimen of *E. parvula* on record, and in his opinion also past records of the infestation of glass-houses by this insect are probably due to the fact that *E. pallidifrons* has been mistaken for *E. parvula*.

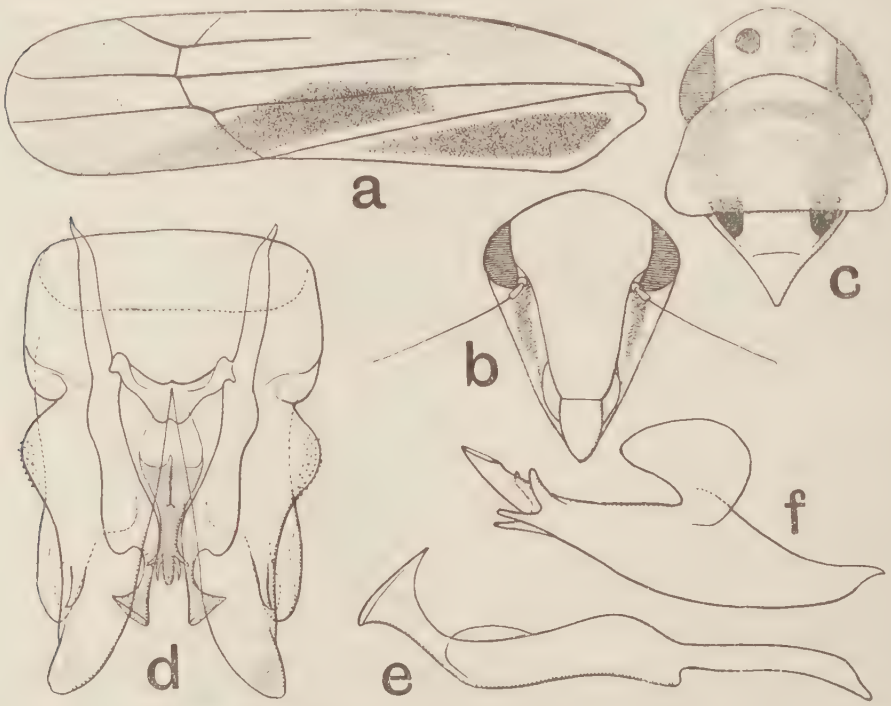


Fig. 2. *Erythroneura pallidifrons*, J. Edw. (Cornwall): *a*, tegmen; *b*, face; *c*, dorsal view of head and thorax; *d*, male pygopher in ventral view; *e*, lateral view of paramere; *f*, lateral view of aedeagus. (*a*, *b*, and *c*, are from ♂ specimen; *d*, *e*, and *f*, are from balsam preparation.)

Methods.

The work in connection with the present paper was carried out in the Zoological Department, Manchester University, and at the University Experimental Grounds, Fallowfield. The material used was obtained from several different sources: Fallowfield, Wilmslow, and Buile Hill Park, Salford, in the Manchester area; and Kew Gardens and Wisley, in the south of England.

The leaf-hoppers were bred on cotton in one of the glass-houses in the Experimental Grounds of the University, and in the laboratory on cotton, primula and geranium. In the laboratory experiments the adults were confined on leaves under lamp-glasses, and the eggs were hatched and the young nymphs reared under similar conditions; as the nymphs became older they became more active and were transferred with leaves to damp filter paper in Petri dishes where they could be more easily examined.

It was hoped that by using material from different localities the two species, *E. parvula* and *E. pallidifrons*, would both be obtained, but in every case the Jassid proved to be *E. pallidifrons*, and the only examples of *E. parvula* which have been examined are pinned specimens in the Manchester Museum.

I should like to thank Dr. H. W. Miles, who suggested the present work, for his helpful criticism and advice. Thanks are also due to Dr. G. H. Rodman, Kew Gardens, Mr. G. Fox-Wilson, Royal Horticultural Society's Gardens, Wisley, Surrey, and Mr. T. Richardson, Buile Hill Park, Salford, for their kindness in supplying living material from their localities; and to Mr. H. Britten, of the Manchester Museum, for the loan and identification of specimens. I should also like to acknowledge my indebtedness to Mr. W. E. China, of the British Museum, for his kindness in separating the two species of leaf-hoppers and for figs. 1 & 2 which he so kindly prepared.

Description of Stages.

Adult.

In "The Entomologist's Monthly Magazine" (1924) Edwards[3] describes *Zygina pallidifrons* thus: "Longer and more slender than *Z. parvula* which it otherwise much resembles and having the frons entirely pale. Length 3·5 mm."

For some time it has been considered possible that *E. pallidifrons* is a colour variety of *E. parvula* and not a distinct species. Mr. W. E. China, however, has very kindly made careful preparations of the two insects and these show very clearly that the species are distinct from one another. Figs. 1 and 2, which have been prepared by Mr. China, show these specific differences; and it will be seen that the male genital apparatus of *E. parvula* is very different from that of *E. pallidifrons*, while both the male and the female *E. parvula* have a claval vein in the fore-wing which is not present in *E. pallidifrons*. The colour differences of the head noticed by Edwards still hold good for the two species.

Egg.

The egg is elongated, about 0·7 mm. in length and slightly curved. It is white, translucent and without distinctive markings on the chorion.

First Instar (fig. 3, *a*).

The 1st instar nymph is approximately 1 mm. in length; it is white and transparent, except for the eyes, which are reddish at first becoming black later. The head is proportionately large and the antennae long, being at least three-quarters of the length of the body. There is no indication of wings except that the hind borders of the meso- and metathorax are slightly concave.

A feature typical of all the nymphal stages of *E. pallidifrons* is the presence of a number of long setae, clubbed at the distal end. On the dorsal surface of the head of the 1st instar nymph there are six of these setae, four along the anterior border and two behind these near the middle line. There is a pair on each of the three thoracic segments and four on the dorsal side of the third to the ninth (inclusive) abdominal segments. There are also some clubbed setae on the front of the head. In addition to the four setae along the crown, which are also visible from the ventral side, there are two rows of four setae between the bases of the antennae, three pairs down the mid-line of the frons and another row of four setae above the hind limit of the frons. A smaller seta, not clubbed, is present under each eye, and there are a few setae of this latter type (1–4) on the frons, posterior to the second row of clubbed setae. The clypeus bears a varying number, up to fourteen, of the smaller setae.

In the 1st instar all the legs are approximately of the same length, and the tarsi have two joints with well-developed pulvilli but no claws. The middle and hind legs have each one of the clubbed setae on the outer side of the tibiae close to the proximal end.

Second Instar (fig. 3, *b*).

The 2nd instar nymph is similar to the first. The length is approximately 1·2 mm. The hind angles of the meso- and metathorax are slightly prolonged backwards giving the first definite indication of the wing-pads. The chaetotaxy of the head and abdomen is similar to that of the 1st instar nymph, but on the thorax, in addition to the setae found in the preceding stage, there is a pair of clubbed setae at the anterior angles of the prothorax, a pair at the anterior angles of the mesothorax and one at the posterior end of each of the mesothoracic wing-pads. The posterior tibiae have an increased number of setae, there being four towards the distal end of the segment in addition to the one found at the proximal end of the tibia in the first stage.

The 2nd instar nymph is still white and transparent with no sign of pigmentation.

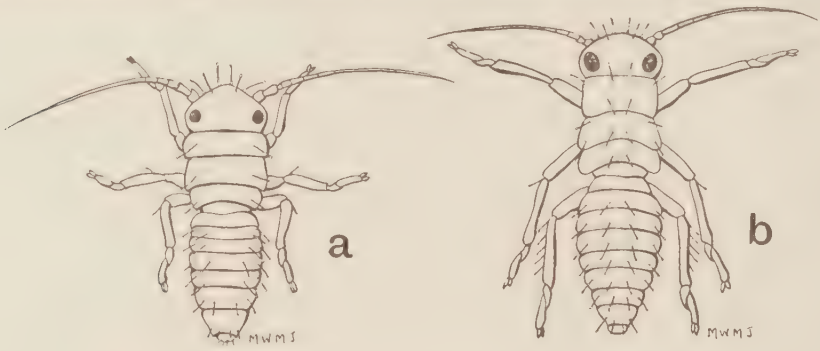


Fig. 3. *Erythroneura pallidifrons* : *a*, 1st instar nymph, x 35 ; *b*, 2nd instar nymph, x 35.

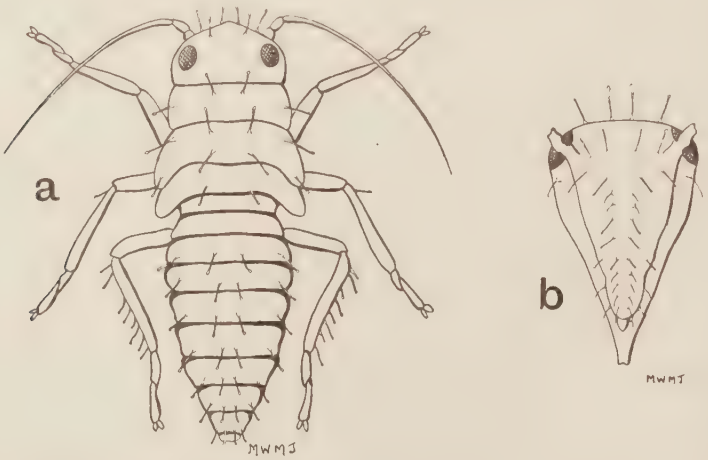


Fig. 4. *Erythroneura pallidifrons* : *a*, 3rd instar nymph, x 35 ; *b*, head of 3rd instar nymph, x about 48.

Third Instar (fig. 4).

The length at this stage is approximately 1·6 mm. The chief difference between the nymphs of the 2nd and 3rd instars is in the length of the wing-pads ; in the third instar the metathoracic pads extend back as far as the second abdominal segment. The chaetotaxy of the body is similar to that of the preceding stage, but on the hind tibiae there are now eight of the large setae.

Fourth Instar (fig. 5).

The 4th instar nymph is approximately 2 mm. in length. The wing-pads are longer than in the 3rd instar. The number of setae on the dorsal surface of the insect has increased; on the thorax, in addition to those found in the earlier stages, a pair of setae is present at the hind angles of the prothorax, a pair at the proximal angles of the wing-pads on the mesothorax, and three setae on the inner border of each of the anterior wing-pads; on the metathorax there is an additional seta on the inner border of each wing-pad. The hind tibiae have now ten setae and the mid-tibiae two.

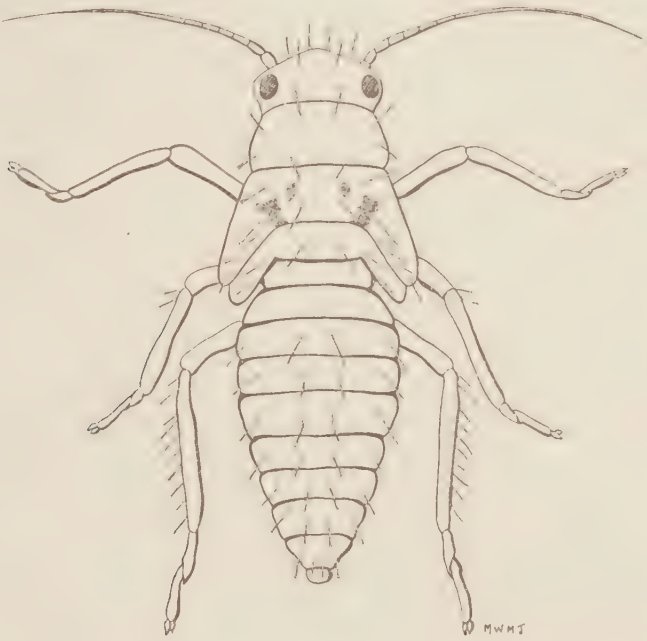


Fig. 5. *Erythroneura pallidifrons :* 4th instar nymph, x 35.

The first sign of pigmentation appears in the 4th instar nymph, there being two patches of dark pigment on the mesothorax, one at the proximal angle of the wing-pads and the other nearer the anterior border of the segment.

Fifth Instar (fig. 6).

The 5th instar nymph is approximately 2·8 mm. in length. The wing-pads are now long and reach about half-way to the posterior end of the abdomen; the pigment on the mesothorax is a little more pronounced than in the 4th instar and the patches of colour are larger, but there is no further pigmentation. There is an additional pair of setae on the prothorax in this stage, on the posterior edge of the segment, and there are now five setae along the inner border of the mesothoracic wing-pads.

In the 5th instar it is possible to distinguish the sex of the insect. The external genitalia of the male nymph consist of a broad basal plate on the ventral side of the abdomen, which bears two short projecting triangular plates from its posterior end. In the female there are two pairs of long pointed plates on the ventral side of the abdomen.

Ecdysis.

At the time of ecdysis the nymphal skin splits along the mid-dorsal line of the head and thorax, and the insect emerges through the slit. The head and antennae are withdrawn first and the abdomen last of all, so that a nymph which has newly moulted can often be found with part of the old skin still adhering to the abdomen. Before the nymph moults the mouth-parts are often inserted well into the leaf tissue to form a firm place of attachment during ecdysis, and because of this the exuviae are frequently found still attached to the leaf. The degree of humidity is of great importance during the moults, for if the old skin becomes too dry, the insect cannot

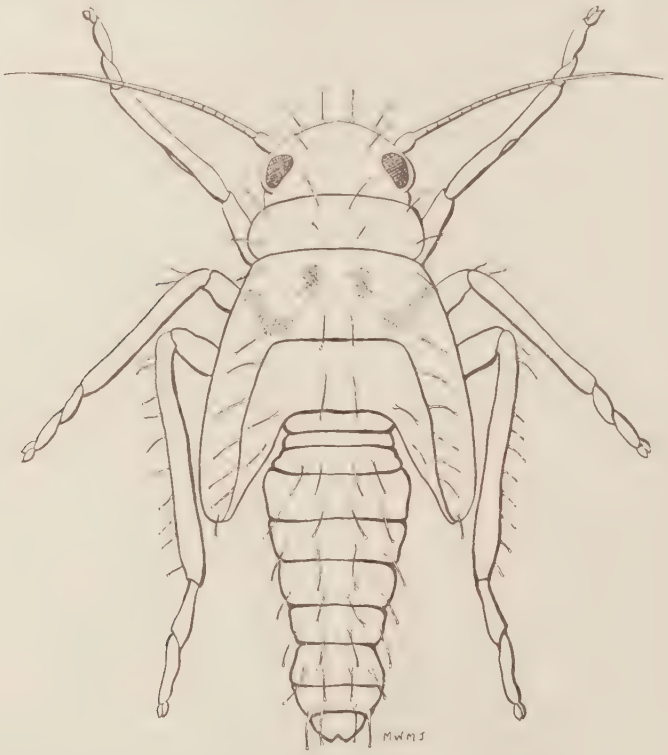


Fig. 6. *Erythroneura pallidifrons* : 5th instar nymph, x 35.

detach itself from it, and if there is too much moisture, the emerging insect cannot harden properly and there is a tendency, especially during the last moult, for it to become stuck to the substratum.

Numerous changes occur at the time of the last moult, which is between the 5th instar nymph and the adult insect. The wings appear, being short at first but rapidly lengthening when the insect has freed itself from the nymphal skin. The clubbed setae, found in all nymphal stages, disappear in the adult, and the antennae are shorter in proportion and the compound eyes larger than in the nymph. At first the imago is colourless, but the pigment begins to appear at once, though it does not develop fully for about 24 hours. In the adult insect the hind legs are very long, being modified for the leaping habit of the JASSIDAE.

Feeding Habits.

Erythroneura pallidifrons has a wide range of food-plants and thus tends to become a serious pest in glass-houses. Both adults and nymphs feed on the leaves, never apparently attacking the stem or other parts; they pierce the cell-walls of the leaf and then suck out the cell-content leaving a bleached area. As a rule the insect feeds on the lower side of the leaf, but the stylets are often pushed right through to the palisade tissue, so that the damage done by the leaf-hopper is often first apparent on the upper side of the leaf. The earliest signs of injury are a series of round white spots on the leaf where the chlorophyll has been removed; each of these represents a single puncture by the insect. As the leaf-hopper continues to feed the spots gradually become confluent and irregular white areas are formed, but the injury appears to be mechanical, as normally it does not spread over the leaf from one puncture. When a plant becomes badly infested the leaves are much soiled by the fluid excreted by the nymphs, which causes further damage, as it forms a very suitable medium for the growth of moulds.

In the nymphal stages *E. pallidifrons* tends to feed on one leaf of a plant only; the first and second stages rarely move when once they have found a favourable place on the leaf. As the nymphs grow the food is used up, so that the older nymphs are obliged to move from place to place on the leaf in search of fresh food. The 5th instar nymphs are fairly active and can run rapidly if disturbed, but even these tend to remain on the same part of the plant.

The adult insects are active, especially in bright weather; they can both fly and leap, though the flights are usually short, from leaf to leaf of the same or neighbouring plants.

Mating and Oviposition.

During copulation the male and female insects lie in the same plane facing in opposite directions.

The eggs are inserted into the leaf tissue of the plant by the saw-like ovipositor of the female. They are almost invariably laid in one of the veins of the leaf on the lower side, though on a very few occasions eggs have been found on the upper side of the leaf. Most frequently the eggs are laid singly, scattered over the leaf, but sometimes they are laid in groups, three to eight eggs being inserted in a row in the same vein. There is no evidence for parthenogenesis and eggs have not been obtained from unfertilised females. Oviposition does not seem to occur often during the day, and as females kept in the dark would not oviposit, it seems probable that most of the eggs are deposited in the early morning or at dusk. The female insects do not begin to oviposit at once after copulation, there being an interval of 7–14 days. After one mating the female leaf-hopper continues to lay fertile eggs for the rest of her life, and on an average lays about 50 eggs.

In this species the oviposition period is very long, from ten days to three months; in most cases it lasted from two to three months, and one female continued to lay eggs at intervals for nearly four months, though in this instance the total number of eggs (10) was very small. The normal rate of egg-laying appears to be from 1–2 a day, though the above-mentioned insect only laid 10 eggs in 113 days, and another deposited 8 eggs in three days. The largest number of eggs laid by one female was 100, which occurred at a constant temperature of 21° C.

At first the egg is not easily visible in the leaf tissue, but as the embryo begins to develop it can be seen as a slight swelling on the vein. The young larva emerges head foremost from the egg, but there appears to be no special mechanism for breaking the chorion and at first the emerging nymph is enclosed in a delicate inner membrane; this membrane usually splits when the nymph is half out of the egg, so that it can generally be found protuding from the empty egg-shell, which remains firmly embedded in the leaf-tissue. The 1st instar nymph begins to feed very shortly after it has emerged from the egg.

Duration of the Life-cycle.

As is common among insects, the life-cycle of *E. pallidifrons* varies in length with the temperature; the following table gives the length of the life-cycle in some of these insects at different periods of the year.

Egg laid	Incubation	1st instar	2nd instar	3rd instar	4th instar	5th instar	Total
	days	days	days	days	days	days	days
24–27.i ...	24–27	11	5	10	9	12	71–74
24–27.i ...	26–29	11	5	8	10	12	72–74
24–27.i ...	36–39	10	10	7	5	17	85–88
12–14.iv ...	14–18	5	7	5	5	9	45–49
13–15.v ...	20–22	4	2	4	4	6	40–42
29–30.v ...	13–14	4	3	4	4	5	33–34
3– 4.vi ...	10–11	5	2	4	6	4	31–32
7–10.vi ...	6– 9	3	4	2	5	5	25–28
10–11.vi ...	12–13	3	4	3	5	6	33–34
17–18.vi ...	13–14	4	4	3	5	11	40–41
24–25.vi ...	13–14	4	5	5	7	8	42–43
10–11.vii ...	17–18	3	5	3	6	11	45–46

Thus the length of the life-cycle varied from 85–88 days (Jan., Feb., March) to 25–28 days (June, July), after which the time lengthened again to 45–46 days (July, Aug., Sept.). The length of the cycle was fairly constant at each season of the year, though there were isolated abnormal insects, such as one individual which hatched from an egg laid on 5th June and took 62-63 days to complete its development, whereas most of the other insects at the same time took approximately 30 days to become mature.

Although, taking a given period, the total length of the life-cycle is more or less constant, the duration of each instar varies considerably in different individuals. In two insects hatching from eggs laid on 14th June, each of which was 42–44 days before becoming mature, the duration of the different stadia were :—

Egg	1st	2nd	3rd	4th	5th	Total
						days
16–18	3	3	4	4	12	42–44
17–19	5	1	5	4	10	42–44

Another group of insects from eggs laid on 10th July gave the following periods for the different instars :—

Egg	1st	2nd	3rd	4th	5th	Total
						days
17–18	3	4	3	6	11	44–45
17–18	3	5	3	6	11	45–46
17–18	3	5	4	7	9	45–46
17–18	4	4	5	7	8	45–46

Thus the lengthening of one of the nymphal stadia may be compensated for by a decrease in the length of another. The duration of the egg-stage appears to be more directly affected by temperature than the other stages and is usually from a third to half of the total length of the development period.

A certain number of leaf-hoppers were bred at a constant temperature of 21° C., and even under these conditions there is a considerable amount of variation in the length of the stadia and of the life-cycle as a whole, though not so much as when the insects are subjected to changes in temperature. At 21° C. the incubation period varied from 9 to 19 days (usually lasting 14–17 days), the first instar from 2–6 days (average 3·5), the 2nd instar 2–5 days (average 3·2), the 3rd instar from 2–9 days (average 3), the 4th instar 3–6 days (average 4·5), and the 5th instar from 4–8 days (average 6·25); the variation in the length of the complete cycle was from 30–32 days to 41–45 days (average 34–37). This variation at a constant temperature is interesting, especially as it was found that eggs laid in the winter (Nov., Dec., Jan.) took from 34–38 days to 41–45 days to reach the last moult, while the length of the life-cycle in insects from eggs laid later (April, May) only varied from 30–32 days to 35–38 days, which suggests that temperature is not the only factor influencing the length of the developmental period of this insect.

Sex-ratio.

In *E. pallidifrons* the female insects slightly outnumber the males, the ratio of males to females being approximately 1–1·3. There seems to be no correlation between the duration of the life-cycle and the sex of the insect.

Preliminary Notes on the Effect of Food-plant Condition.

Some preliminary experiments were carried out during the summer of 1930 on the infestation of cotton plants by *E. pallidifrons*. Four blocks of cotton seed (American Upland), each block containing 20 plants in 12 ins. pots, were sown; two blocks, A and B, on 27th March 1930 and the other two, X and Y, on 8th May. A, X and Y, all received 1,000 cc. of water a week, while B only received 500 cc. The soil in the pots belonging to blocks A, B and Y, was left untouched, but the soil in the remaining block, X, was tilled after each watering.

Infestation counts of the Jassids were taken at intervals of seven days. The system used in making the counts was similar to the methods given in other papers dealing with the infestation of cotton by Jassids: that is, the infestation factor is indicated by the number of nymphs on a stated number of leaves in each block; in the present instance 20 leaves in each block were examined at each count.

Infestation counts on blocks A and B began on 5th May, when the cotton plants were about five weeks old. Counts on X and Y began on 23rd June.

The mean infestation factors for the four blocks of plants for the period of the experiments (about 24 weeks) were as follows:—

A. 5·5 nymphs to 20 leaves.
B. 3·0 ,, ,, ,,
X. 1·8 ,, ,, ,,
Y. 1·8 ,, ,, ,,

Block A, planted in March and receiving 1,000 cc. of water a week, has thus a definitely higher infestation factor than block B, also planted in March but only receiving 500 cc. a week. Both these blocks show a considerably higher degree of

infestation than the plants sown in May. The infestation of X and Y is the same, so that tilling the soil appears to have no effect, either adverse or favourable, on the infestation of the plant by *E. pallidifrons*.

The infestation factors for all four blocks of cotton are low, but this is partly due to the fact that the temperature of the glass-house was so high during the early and middle part of the summer that it proved to be unfavourable for the development of the Jassids, and for a time in the middle of the experiments the insects almost disappeared from the plants.

Parasites.

Only one species parasitic on *E. pallidifrons* was obtained. This was a Mymarid, not yet identified, which was found to be parasitic on the egg of the leaf-hopper. The parasite has been bred from eggs from two localities, Fallowfield, Manchester, and Wilmslow, Cheshire, but it has not so far been possible to breed it successfully in the laboratory. It is interesting to note that Mymarid parasites, in each case belonging to the genus *Anagrus*, have been recorded from the eggs of leaf-hoppers in Sweden[20] and in California and Idaho[19].

Economic Position.

E. pallidifrons and the nearly related *E. parvula* are reported with increasing frequency as pests on plants in glass-houses. They are widely distributed in this country and have a very wide range of food-plants. *E. pallidifrons* will feed on *Chrysanthemum*, *Gossypium*, *Fuchsia*, *Geranium*, *Nicotiana*, *Primula* and *Salvia*, while in addition to the above plants, *E. parvula* has been recorded from *Asparagus sprengeri*, *Calceolaria*, Lemon-scented Verbena, *Salpiglossis*[15] and tomato[10]. The injury to the plant appears to be similar in every case, the leaves becoming covered with bleached patches caused by the removal of the chlorophyll by the insect.

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NOTES ON THE *SARCOPHAGA PEREGRINA* GROUP (DIPT.).

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Illingworth (1926) published his experiences with *Sarcophaga fuscicauda*, a fly regarded by him as being of medical importance, and he also suggested it was being transported over the Orient by shipping. There can be little doubt concerning the identity of the fly, this being identical with that published under the same name by Senior-White (1924); both authors included Queensland in its distribution.

Subsequently I pointed out (1927, p. 435), that the name *fuscicauda* represented more than one form as applied in literature and to this complex I gave the name *peregrina*-group. I was able to distinguish three distinct species and four names that applied to it; I had not seen, however, the original species from Formosa, *Sarcophaga fuscicauda*, Bött.

Senior-White (1930, p. 74) has accepted the new name I then gave to the Javanese species, admitting he had it combined with *fuscicauda* from India, and he pointed out that Parker made the same error. He is not convinced of the specific status of the Australian form that stands under the name *peregrina*, suggesting it may be conspecific with *S. karnyi* of Java.

I am in accord with Senior-White when he questions whether *fuscicauda*, Bött., and *hutsoni*, Parker, are conspecific; and in addition to this it seems almost certain that Illingworth is correct in regarding *S. irrequieta*, Walker, as not being conspecific with *S. peregrina*, Desvoidy, the latter being that species to which Johnston & Tiegs had applied the name; *S. irrequieta*, J. & T. (*nec* Walker), is identical however.

Illingworth had specimens identified for him as *S. fuscicauda* compared with the type of *S. irrequieta*, Walker, a female from Western Australia, and the comparison yielded two points of difference, namely, in the type the intermediate pair of prescutellar bristles (*i.e.* the prescutellar acrostichals) were absent and the frons was undoubtedly wider. These differences compare favourably with those to be found in *S. tryoni*, J. & T., but that species is not yet known to occur outside the Queensland Coastal area. *S. froggatti*, Taylor, is the only other species known to me that can possibly be conspecific with the type of *S. irrequieta*, Walker, judging from this information.

More synonymy that stands under *S. peregrina* cannot be adequately discussed at present. The names were placed there by Johnston & Tiegs, and with the exception of *S. frontalis*, Macquart, from Dutch New Guinea, their descriptions were based on Australian specimens, so they could hardly belong to the *peregrina*-group if they are wrongly placed.

Those forms already examined may be distinguished by the characters given in the following key :—

1. Sheath of aedeagus with an appendage on the rear. India & Ceylon *hutsoni*, Parker

   Sheath of the aedeagus without such an appendage, smooth 2

2. The inner processes which arise between the sheath and the anterior appendage, when seen ventrally, formed by two pairs of crescent-shaped figures (Johnston & Hardy, 1923, p. 123, fig. F, *i.p.*). Australia *peregrina*, Desv.

   The inner processes, seen ventrally, formed of only one pair of simple, perhaps filament-like, figures, coming to a more or less acute point; the actual shape, however, is not understood, but stands very clearly contrasted with that of the above (Hardy, 1927, p. 454, figs. E & F, *i.p.*). Java ... ... *karnyi*, Hardy

The inner processes of the aedeagus on *S. hutsoni* again differ, so it would seem necessary to observe this structure for the determination of all the forms within the group. There are some difficulties to be overcome in this, because they would need dissecting out in order to find their correct shape and structure.

An examination of the puparia belonging to these three forms shows the same general tuberculations around the posterior spiracles, but in the smaller details *S. hutsoni* differs from the other two more than those two differ from each other. Doubtless larval characters will be found to support the specific status of all three.

It is the habits of these flies that make them worthy of special report. Presumably all the forms breed in human faeces, as pointed out by Illingworth, and hence they become closely associated with mankind. Their relation to human faeces and human food may hardly affect Australia, for the adult does not normally frequent dwellings there, but Illingworth considers them important in this connection in the Islands. *S. peregrina*, Desv., is the only species in Australia that has this breeding habit so far as yet known. Not infrequently it will also attack carrion that has become tainted; thus it competes in Brisbane with *S. tryoni*, *S. froggatti*, *S. misera* and occasionally other species of this genus. In four years breeding, I have had it five times under more or less normal conditions in carrion, but in addition to this several cases were met with when gathering data on the relation between temperature and pupation. Johnston & Tiegs (1922a, p. 87) also had some scanty records which they summarised. Johnston & Hardy (1923a, p. 40) gave full details of some specimens bred in midwinter, a summary being given in the following table, together with four records that subsequently accrued.

Number of specimens bred	Date of deposition	Number of days in carrion	Number of subsequent days to pupation	Number of days in puparium	Number of days to complete metamorphosis
	1922				
7	2nd June	18–21	3–9	65–106	86–124
	1923				
20	6th March	5	1	9–10	15–16
2	9th Oct.	2	0–1	10–11	13
	1925				
10	1st March	3–4	2–3	12–14	18–21
2	15th Dec.	6	3	12	21

The number of days that maggots remain in carrion does not necessarily bear relation to the time of feeding there. The period of feeding seems to be normally three days, but the maggots may fail to leave till some time after. One record above gives two days spent in the carrion and the maggots pupated almost immediately after. I was disposed to regard this as a case where the carrion had been contaminated before being used for experimental purposes, but *S. peregrina* does not readily come to carrion for oviposition, despite the fact that it is one of the dominant species, and in addition to this I could not find any evidence to support the supposition that the isolation of the carrion before it was used differed from that of any other case handled by me. All carrion was isolated whilst fresh under conditions that precluded contamination until wanted.

Temperature and pupation experiments resulted in the rather striking results given below. The incubators were electrically controlled and built up with sawdust and paper as insulating material between wood, and in addition they were lined with

asbestos. There was ample ventilation allowed for, yet the incubators varied not more than one degree of that set except on rare occasions that do not affect the present records. Also there was a slight unavoidable temporary drop in daily temperatures when the incubators were opened to take out and put in jars containing the puparia or maggots under investigation. The following table gives results obtained for *S. peregrina*.

Temperature (Fahr.)	Number of specimens bred	Number of days in puparium	Number of days the majority (in brackets) remained in the puparium
65°	16	19–28 and 64 (1)	19–23 (11)
70°	10	15–20 and 54–79 (5)	15–20 (5)
75°	15	10–14 and 25 (1)	10 (10)
80°	14	9–10	9–10 (14)
84°	7	8–9	9 (5)
85°	49	7–10	8 (36)

It will be seen that there is a tendency for the puparia placed at 70° F. and lower to become divided into two sets, one emerging early, the other awaiting an interval before completing metamorphosis. I have included in brackets the numbers recorded in the latter case but actually there were six puparia to emerge when the experiment at 70° F. was discontinued; these had been in the incubators for 89 days, showing that the maximum duration at 70° is much longer than that given in the table, and the majority therefore had delayed emergence till the second batch. I believe this discontinuity in sequence of emergences to be quite normal, for it was also noticed in other species of the genus where larger numbers were bred. Probably a few intermediate emergences would have filled the wide gap between these discontinuous records had their numbers been large enough, nevertheless the tendency for the division would have still remained quite perceptible. Of 14 specimens placed at 80° F., seven completed their metamorphosis in nine days and seven in ten.

The minimum time spent in the puparium in these experiments is shown to be seven days for two flies, but normally it is eight, which number is given by Johnston & Tiegs for the summer months. The maximum number of days in the puparium is recorded as 79, at 70° F., and 124 days is recorded for normal breeding in mid-winter.

There are some records of puparia that were placed under incompleted incubation experiments and are referred to above. Daily temperatures outside the incubators began to exceed 70° F. and thus caused a rise within the incubator spoiling the consistency of temperatures, so the incubator affected was reset at a higher figure, the contents being allowed to complete metamorphosis at room temperatures. After being in the incubator for 89 days, the six remaining puparia eventually emerged from the 6th September up to the 6th October, emerging in 96 to 120 days, thus remaining in the puparia up to 30 days over September, which is a comparatively warm month.

One can only conclude that some specimens hibernate in the puparium through the winter months, whereas others deposited at this same time emerge as flies during that season. During the warmer periods of the year each batch of maggots deposited would complete their metamorphosis within a small variable limit, whereas deposited

in the winter they vary greatly in the maximum and minimum number of days taken to complete metamorphosis, the stage at which greatest variation occurs being that of the puparium. Total life periods show up to 6 days variation for March and nearly 40 days for June, whilst the puparia subjected to consistent temperatures show a variation up to 3 days at 80° Fahr. and above, 15 days at 75°, 64 at 70°, and 45 at 65°.

It is of interest to contrast this with some results obtained with similar experiments using Calliphorine flies. The latter varied most in the duration of the prepupal period, compared with which the pupal stage is found to be very consistent at all temperatures in the incubators. The more one reduces the temperatures and incubators towards that at which development ceases, the greater becomes this variation in time periods; and it would seem that whereas *Sarcophaga*, in the main, cease development in the puparium at higher temperatures than those affecting the maggots, the Calliphorines continue to develop in the puparium at lower temperatures than they do in the prepupal stage. This would indicate that those *Sarcophaga* hibernating at winter temperatures comparable to those of Brisbane do so in the puparium, whereas most hibernating *Calliphora* and *Lucilia* would spend the winter mainly in the maggot form.

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NOTES ON TWO LOCUSTS OF MINOR ECONOMIC IMPORTANCE IN THE SUDAN.

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The so-called short-horned locusts are frequently, for convenience sake, regarded as comprising two classes: the true locusts (Arabic: Girad) and the short-horned grasshoppers (Arabic: Gabura). It is difficult, however, to find definitions of these classes by means of which every species may be correctly assigned to its true place. The swarming habits of the true locust are often cited as connoting this class only, involving, as these habits do, the periodical appearance of excessive numbers of both hoppers and adults. Moreover the true locust is gregarious, in that the hoppers move in bands from one place to another, and the adults fly in vast swarms often over long distances. The fact that the grasshoppers are solitary in habit and manifest mutual independence of action is often taken as their chief distinguishing character. There is no doubt that these features do partly separate these two classes of insects from each other, but there are certain species which appear to occupy a position intermediate between the two. One normally solitary may, in certain circumstances, multiply rapidly and give rise to hoppers, which in certain respects act like those true locusts. Moreover the winged adults may undertake short massed flights resembling the migrations of swarms. On the other hand the fact, now fully established, that most true gregarious locusts have their solitary forms, which never associate, places even them in this respect with the grasshoppers.

The two species dealt with here seem to occupy such an intermediate position. The Tree Locust (*Anacridium moestum*, Serv.), known in Arabic as Sari-el-lel owing to its propensities for movement by night, is usually an insect of solitary habits which lives in or near trees. Nevertheless it has been known in certain years to give rise to hoppers of a swarming type, and in the adult stage to undertake flights in swarms, the length and duration of which however are unknown. The Brown-spotted Locust (*Cyrtacanthacris tatarica*, L.), though even more truly solitary, may also in some seasons breed rapidly, and the hoppers have been found wandering in loosely aggregated bands searching for food. No mass movements of adults have been recorded, and this species only slightly transgresses the limits of the true grasshoppers.

As regards their position economically both species are potential pests of some importance, but the damage they cause is intermittent rather than regular, and can in no sense be classed in extent with that done by the true migrant locusts. As a pest in the Sudan the Tree Locust is considerably the more important of the two.

The Tree Locust (*Anacridium moestum*, Serv.).

Four species have been described under the genus *Anacridium*, namely: *A. aegyptium*, L., *A. moestum*, Serv., *A. flavescens*, F., and *A. arabicum*, Uvar., the last named recently described by Uvarov from Arabia. The first, which is the genotype, and is well known as a pest of tobacco and other crops in South Europe and North Africa, is a Mediterranean species which is not known to occur south of Upper Egypt. It has not been found in the Sudan. *A. flavescens* appears to be confined to the Indian peninsula. *A. moestum* is essentially an African species and one which appears to have a wide range of distribution on the continent. It has been subdivided into

two very well defined subspecies: *A. moestum moestum*, Serv., and *A. moestum melanorhodon*, Walk. These, according to Uvarov,[4] must be regarded as geographical races. As will be pointed out later, they meet and overlap in the Sudan. It is with the latter of these subspecies that we are concerned here. The former will be referred to later.

Geographical Distribution.

A. moestum melanorhodon is to be regarded as a northern race in Africa, whereas *A. moestum moestum* occurs throughout South Africa and the more open forest land of Central Africa. The subspecies was originally described from Cape Verde Islands and according to Uvarov,[4] other known localities outside the Sudan are Massowah, Aden, Sokotra and Abyssinia. Vayssière & Mimeur[7] record it from St. Louis (Senegal) as well as from points further inland, Kayes and Timbuktu being named. It has also been noted from the Central Sahara.

In the Sudan the subspecies has a wide range. On the east it has been recorded from the Red Sea maritime plain, and has been noticed breeding regularly in the Red Sea hills. From there it extends south as far as Eritrea and on the west through Kassala to the Nile. It would appear to be most abundant in the south-west (Darfur and Kordofan), where it has much more the status of a pest. From Khartoum it may be traced south by a continuous series of authenticated records up the Blue Nile to Abyssinia. In the Gezira district, between the Blue and White Niles, it is a very common insect. In the basin of the White Nile it has been taken as far south as Lat. 5° N. (Rejaf and Mongalla districts), but here, judging from material collected in the southern portions of the country, *A. moestum moestum* is the prevailing form. Certain intermediate specimens may indicate the occasional interbreeding of the two races, but direct evidence on this point is lacking. North of Khartoum it occurs wherever a suitable habitat is found and as far as the northern frontier.

It should be noted that the main factor which determines the distribution of this species is the presence or absence of certain kinds of trees. Though it is to be found occasionally among cultivated crops at most times of the year, it is essentially a tree-loving insect, its chief habitat being among the natural thickets of *Acacia* which grow in the drier parts of the Sudan, and it is seldom seen far removed from trees, to which it resorts at frequent intervals. Extending completely across the Continent is a zone of vegetation of which an important component are trees of the genus *Acacia*. According to Shantz & Marbut[3] this zone in the north, roughly along a line in the neighbourhood of 16° N. Lat., is composed of *Acacia* trees and short desert grass, but further south "tall grass savanna" takes the place of the short grasses. Further enquiry therefore may establish the occupancy of this entire vegetation belt by *Anacridium*, and the movements of these locusts within this belt may prove to be more frequent and of longer duration than has hitherto been supposed.

Literature.

Whilst a considerable amount of information exists with regard to *A. aegyptium* very little is known regarding *A. moestum*. *A. moestum moestum* has been stated to form swarms in the Orange Free State,[5] and to cause severe damage to fruit trees in many parts of the Union. Nothing whatever seems to be known regarding its bionomics.

A. moestum melanorhodon has been recorded by Vayssière[6] as forming swarms in French Equatorial Africa to such an extent as to cause a confusion between this species and *Schistocerca gregaria*. Vayssière & Mimeur[7] include it among pests of cotton in French West Africa and give a short description of the adult.

Johnston[2] included certain notes on this species in a popular paper on locusts written in 1924.

The Existence of Phases in Anacridium moestum.

The existence of a solitary and a swarming phase has now been established for at least three of the most important migratory locusts of the Old World. The former is distributed throughout the area of occurrence of the species, and at certain times gives rise to swarms which migrate over or beyond this area. It is of importance to know how far this obtains in the case of those species which are on the border-line between the migrant locusts and solitary grasshoppers.

In the Sudan two forms of *Anacridium m. melanorhodon* have been observed. The first is the better known solitary form, rarely observed gregariously except in winter, and occupying a very wide range in the country. The other has been seen on one occasion only, within the experience of the writer, in the Northern Sudan in 1924. In the summer and autumn of that year this locust assumed a kind of swarming condition, larvae of a different appearance were produced, and the resulting adults were smaller, particularly the females. It must be remarked, however, that apart from these differences in actual size there appear to be no structural differences such as are known for example to exist so strikingly between the phases of *Locusta migratoria*, L.

Description of Anacridium melanorhodon.

Adult.—The adult locust is a large and strongly built insect. The general body colour is dull brick-red. The elytra are greyish. The head is frequently lighter in colour than the remainder of the body. Antennae dark, frequently almost black. Eyes dull red, large and prominent, occupying more than half the length between the vertex and the lowest point of the gena; a dark sub-ocular streak bounded by whitish lines extending from the eye to the lower margin of the gena; a median white line on the epicranium. Pronotum usually dull red, often mottled laterally with a lighter colour; disc slightly convex, with a low keel, which is cut by three deep sulci; the keel with a median light red line; hind margin broadly rounded, the metazona finely punctured and with several diffuse white tubercles dorsally and laterally. Elytra long, moderately narrow and with attenuate apices. Wings with an indefinitely margined band or fascia near the anal angle varying in colour from dull brown to black, and varying also in size, being often almost obsolete; a few faint spots, or lines between the anal and axillar veins, and again at the apex; between the wing-fascia and the insertion of the wing is a more or less strongly marked suffused purple coloration. Hind legs with broad and strong femora, reddish on the inner surface and with three dark areas on the upper surface; tibiae purple, with ten or eleven strong black-tipped spines on the inner margin, and eight on the outer; tarsi with well developed pulvilli. Prosternal spine laterally compressed and tapering towards the apex on the front margin; hind margin straight.

There is no difference in appearance between the sexes except in the matter of size, the male being usually some 10 mm. smaller than the female in total length.

First Stage Larva.—Colour grass-green. Length, shortly after emergence, 5–6 mm. Basal joints of the antennae dark green, apical six joints brown. Eyes black or very dark brown. Pronotum distinctly keeled. Brown spots cover whole body on the dorsal surface.

As there is some danger of confusion in the field between the 1st stage larva of *Anacridium melanorhodon* and the green form of the similar stage in *Schistocerca gregaria flaviventris*, it may be useful to point out certain differences between them.

Anacridium melanorhodon.	*Schistocerca flaviventris.*
(Normal 1st stage larva.)	(Green form of 1st stage larva.)
1. General colour leaf-green.	1. General colour yellow-green.
2. Tips of antennae brown.	2. Antennae wholly light-coloured.
3. Lower margin of pronotum relatively lower and descending obliquely towards the abdomen.	3. Lower margin relatively higher and more parallel with the keel.
4. Front margin of the pronotum approximating closely to the eye.	4. Front margin more distant from the eye.
5. Eyes dark.	5. Eyes light-coloured.

Second Stage Larva (*swarming*).—About 12 hours after moulting, length 10–12 mm. Head pale green covered with small black spots, mouth-parts green ; black area on the vertex between the eyes, which is continued beneath the eye in a black streak running to the lower margin of the gena ; eyes brown. Basal two joints of the antennae green, remainder black, except the apical four or five joints which are light brown. Pronotum keeled, with a narrow median white line ; two black areas on each side of the keel ; diffusely black-spotted laterally. Abdomen with small black markings on each segment ; a row of black marks forming a well-defined line on the median dorsal surface. Legs green ; hind femora with two black areas on the upper surface ; tarsi fuscous. Ventral surface of the body light green.

Second Stage Larva (*solitary*).—It may be noted here that in the case of a larva which is kept solitary from the time of emergence, certain definite colour differences become apparent after the first moult. These consist essentially in a reduction of the black markings on the body, particularly on the pronotum and femora, where the black areas tend to become obsolete.

Sometimes during the period occupied by the 2nd stage the general colour of the normal larva changes to a duller green shade.

Third Stage Larva (*swarming*).—Three days after the moult, length 15–18 mm. Colour yellowish green. There is a notable change in the shape of the larva at this moult, owing to the keel becoming more convex and thus giving a deeper appearance to the pronotal region. The disproportion in the size of the head apparent in the 1st stage has disappeared. There is also an extension of the black areas, which are as follows :—Head : vertex and sub-ocular streak. Pronotum : along the keel and at the lower angle. Abdomen : strong dorsal and lateral lines. Hind femora : upper surface.

Third Stage Larva (*solitary*).—The colour is pure green without the yellow tinge possessed by the crowded larvae. The black markings have almost totally disappeared, with the exception of the black streaks under the eyes. These often lighten to a blue colour.

Fourth Stage Larva (*swarming*).—Average measurements : Total length 32 mm., length of pronotum 9 mm., hind femur 17 mm. Colour greenish yellow. Antennae black, except tip which is yellow. Frons and mouth-parts diffusely black-spotted ; the black bands on the vertex and under the eyes persist ; eyes bluish in posterior half. Pronotum on its hind margin narrowly white, with a line of black spots on inner side of the marginal white line. Distal portions of tibiae and the tarsi dark. Abdomen with a strong white lateral line in which lie the spiracles, and above which is an elongated black streak on each segment.

Fourth Stage Larva (*solitary*).—Here again the black markings are wanting and the colour is bright leaf-green, with the exception of a yellow area between the eye and hind margin of the head, and the blue streaks beneath the eyes.

Fifth Stage Larva (*swarming*).—Very similar to the preceding stage except that there is a great increase in size. The black wing-veins become clearly marked. The

colour is, as previously, yellowish but more intensely so, with three main black areas more or less clearly defined on the head, pronotal keel and abdomen. Broods have been met with in the field which possess a red suffusion over the greater part of the body in this stage.

Solitary larva like the larva of 4th stage.

The description of the adult given above is that of the form usually encountered throughout the Sudan. Its larvae are green and are found on trees and bushes as well as occasionally on ground vegetation. The larvae described above, which were met with in 1924, and which are referred to as the "swarming" form, turned to an adult which it has been found difficult to separate from the usual form on any character except size. The following may be given as a description of this form: Strongly resembles that already described, but is smaller in both sexes. Head, pronotum, meso- and metathoracic segments frequently of various lighter brown colours giving these portions a variegated or marbled colour. There is somewhat less difference between the comparative size of the sexes in the two forms. On the average of a large number of measurements, the female of the solitary form is larger than the male by 12 per cent. of its average length, whereas the swarming form gives 5·5 per cent.

Measurements of the two forms give no structural difference of any importance. The ratio $\frac{E}{HF}$ varies only from 2·29 (swarming form) to 2·18 (solitary form), showing no appreciable tendency to lengthening of the elytra and organs of flight in the swarming form. Observations in the Sudan tend to show that this species does not undertake long migratory flights, though flight in swarms has been recorded frequently.

A statement of measurements is given in Table I.

TABLE I.

Comparative Measurements of the Swarming and Solitary Forms of Anacridium moestum melanorhodon, *Walk.*

Locality	Date	Number of specimens	Total length	Length elytra	Length hind femur	Length pronotum	Depth pronotum	Breadth pronotum	Breadth head	Ratio $\frac{E}{HF}$
Swarming form Khartoum	x. 1924	39♂	68·75	57·00	25·37	10·25	8·75	5·87	6·50	2·24
		51♀	72·57	60·50	26·35	10·78	9·42	6·28	6·64	2·29
Solitary form Medani	iii. 1922	10♂	77·7	64·2	27·5	11·2	9·7	6·7	7·2	2·33
		9♀	90·0	74·0	32·5	13·0	11·5	8·0	8·0	2·27

Comparison of Adults of A. m. melanorhodon and Schistocerca gregaria flaviventris.

When once carefully compared there can be no difficulty in separating these two species. Mr. Uvarov however assures me that confusion has occurred and M. Vayssière[6] refers to this as happening in French West Africa.

In all probability between *A. melanorhodon* and the swarming phase of *Schistocerca gregaria* confusion has not taken place in the Sudan, since the two species differ very widely in outward appearance and habitat. Moreover the native residents are aware of the difference, since they have separate Arabic names for the two species

S. gregaria being known as Girad-el-rihal (migratory locust) and *A. melanorhodon* as Sari-el-lel (night wanderer) from its nocturnal flying habits.

On the other hand confusion may occur between this species and the solitary phase of the Desert Locust (*S. gregaria flaviventris*) owing to their somewhat similar superficial appearance.

It may be useful to give in tabular form the chief differences between them. These are partly adapted from Uvarov.[4]

Anacridium moestum melanorhodon.	*Schistocerca gregaria flaviventris.*
1. General colour reddish.	1. General colour relatively greyer.
2. Antennae black.	2. Antennae light in colour.
3. Prosternal spine bent back and laterally compressed, pointed.	3. Not bent back, blunt and rounded.
4. Hind tibiae purple with strong reddish spines.	4. Hind tibiae yellowish or light-coloured.
5. Wings with an infumate band at anal and purple suffusion within.	5. Wings hyaline or with a yellow suffusion at anal angle.
6. Male subgenital plate trilobate.	6. Male subgenital plate bilobate.
7. Male cerci longer than anal plate.	7. Male cerci shorter than anal plate.
8. Relatively larger and stronger.	8. Relatively smaller and less stoutly built.

It may be noted also in this connection that the recently moulted adult of *S. gregaria* is reddish in colour, a fact which might lead to confusion by the untrained observer.

Habits of Adults.

The adults are usually encountered singly in the localities in which they occur. These localities are chiefly areas covered by a sparse growth of *Acacia* and other trees with or without a close low ground vegetation. This locust also occurs in cultivated areas, but these individuals are immigrants from without, or have invaded crops from surrounding trees, on which they normally live. During the day they usually remain motionless on the branches and on the shady side. When approached they often move round the branch away from the spectator and readily take to flight. When driven into an open space, however, they always break back to the trees.

Breeding is confined, in the Northern Sudan, to the summer or periods of rains, and there is only a single brood.

In the winter this species manifests a peculiar gregarious habit. During the period November to March trees, particularly species of *Acacia*, may be found harbouring large numbers. These are by no means dormant, since they are easily disturbed by day and take to flight readily. They rest along the branches of trees head upwards. Observed by night they occur in the lower parts of the trees, but ascend to the tops at sunrise presumably to catch the early rays.

Where no trees exist they may be found in and under low bushes and even shrubby vegetation. A particular case may be mentioned in illustration. In an isolated locality devoid of trees between the Blue and White Niles on 16.i.1930 hundreds of adults were found on the lower portions of, and on the ground underneath, small shrubs of *Cadaba rotundifolia*. No larger trees were visible, and a few xerophytic plants and tufts of grasses formed almost the sole remaining vegetation, with the exception of some native-owned cotton plants which had been sown in the rains in September previously. The locusts were large in size, the wings showed a strong reddish suffusion at the base, as did the pronotum and inner surface of the hind

femora. The locality was visited again on 13.iii.1930 and no locusts were found under the bushes. Search in the immediate vicinity revealed many single individuals. It appears probable that with a rise in temperature, which took place at the end of February, these locusts scattered. A certain amount of damage was done by them to the adjacent cotton plants at this time. No evidence was obtained of copulation, and the internal sexual organs were not mature. The insects were certainly in diapause. Measurements of specimens from these winter groups are here given.

TABLE II.

Date	Locality	No. of specimens	Total length mm.	Pronotum mm.	Elytra mm.	Hind femur mm.	$\frac{E}{HF}$ mm.
16.i.30	Wad-el-Shegil ...	51 ♂	80	12	69	29	2·37
		70 ♀	91	14	78	34	2·29
19.iii.30	Rufaa	15 ♂	80	12	68·5	29	2·36
		15 ♀	89·5	13	74	32·5	2·27

It is in the winter and during the period of gregarious existence that the adults attack cultivated trees. An instance of this kind occurred in the Khartoum district in the winter of 1923. *Anacridium* larvae had been very common among *Acacia* near the Nile during the previous autumn, and the adults had remained among these trees till December. During this month they migrated to certain plantations of limes and guavas in the neighbourhood, which they more or less completely defoliated. By the end of February they had moved away from the fruit trees, and after spending some days among the surrounding *Acacia* thickets retired completely from the river districts.

The life-history after the dispersion of the sedentary swarms is normally as follows in the Northern Sudan. The adults frequent trees during the spring months, which are the driest and hottest, and pairing usually is noticed commonly in June, by which time a little rain may have fallen in some places. Scattered flights have been noticed during this month. Females containing eggs in some years are common by the early days of July. North of about Lat. 14° N. oviposition becomes general from the end of July in places where rain has fallen. It is believed that the date of pairing and copulation depends on the occurrence of rain. After the first shower pairs are to be found *in copula*. Females thus taken have generally laid eggs from 10 to 20 days later.

South of Lat. 14° N. with the earlier incidence of rains, pairing takes place earlier. Thus in the south-west Sudan movements of adults have been observed in April and May and pairing in May. Eggs may be laid here also from this month onwards during the summer.

Egg-stage.

The female lays in damp sand. The egg-pod, which is surrounded by a moderately firm cemented coat of sand, measures about 75 mm. in length and contains usually 150–200 eggs. Each egg measures approximately 6 mm. long and is somewhat curved. They are bright yellow in colour on being laid, but shortly after the chorion, or outer coat, changes to brown.

In cages one to three egg-pods are laid by each female, and the species is usually single-brooded in the Northern Sudan. In the southern parts of the country, where the season of rains is prolonged, there is evidence of a second or partial second brood.

The incubation period varies much more than in the case of the true swarming species, from 23 to 65 days having been observed as the mimimum and maximum. No evidence of diapause in this stage has yet been found, since all egg-pods which have failed to hatch have on examination been found to be dead. There may, however, be some factors which favour such a diapause in the field, though this is unlikely.

No parasites or predators of the egg have been noticed.

Larval Stages.

The manner of hatching appears to be little different from that of other species of locust. The shed skins of the earliest, or intermediate, moult are cast on emergence from the egg burrow and litter the ground at its entrance. The young larvae immediately become active and climb the nearest plant or tree. They are negatively geotropic and in cages strongly positively phototropic.

Young larvae have been fed for some days after emergence on sedge and other grasses, *Cyperus* and *Panicum*, but later ceased feeding and had to be given the leaves of trees, *Zizyphus* or *Acacia*. This would seem to point to the newly emerged larva being able to subsist on common types of ground vegetation during the search for its normal food.

Larvae in cages do not feed for the first 24 hours after emergence from the egg, and during the first and second stages they feed sparingly. It is only in the third and following stages that feeding becomes more continuous, and a consequent more rapid increase in size takes place.

The length of the larval stages from hatching to last moult is very variable, 48 days being the minimum at present observed and 69 the maximum. The three later stages usually extend over approximately the same length of time as the first two, provided that conditions remain the same throughout.

The normal food of this locust is the leaves of various trees. Those of the genus *Acacia* are the most sought after. Another favourite tree is *Zizyphus spina-christi* (Arabic : Siddir), and larvae can be reared most readily in captivity on this food. To these must be added a number of cultivated fruit and shade trees, in particular the lime and various species of *Ficus*. A tree frequently cultivated in gardens which is very often selected by the larvae and defoliated is *Pithecolobium dulce*. *Balanites aegyptiaca* has also been attacked. Cotton is occasionally attacked, mainly by moving swarms of adults. In one case a swarm attacked cotton during two days in the Gezira district and afterwards disappeared. There were no trees however at hand, and little vegetation with the exception of tall grasses.

One peculiarity of the larvae is that they feed by night. A hungry hopper will, however, feed at any time. Trees have been observed to be largely defoliated during one night. During the day the larvae usually rest on the branches. They are very wary and when approached will move round the stem away from the observer. Sometimes also they drop down into the undergrowth for concealment.

Larvae seem to move upwards for feeding, with the result that the upper and younger portions of trees are defoliated in a very characteristic manner. Where the number of larvae present is large, the trees are usually entirely stripped. The barking of young *Acacia* trees by the larvae has been observed on several occasions.

A certain amount of preference is shown by larvae in the selection of food. In one case where trees of *Acacia ehrenbergiana* and *Zizyphus spina-christi* were growing together, only the latter was attacked, whereas in other localities the former was also eaten.

The leaves of the food-plant are usually attacked from the edge and entirely eaten away. Young individuals often puncture holes and eat round within the circumference.

Natural Enemies.

As has been remarked, no enemy of the eggs has been found. The larvae, from their habit of living in trees armed with spines, are probably to some extent protected from enemies, particularly as the tendency of both larvae and adult is to retreat to the inner and thicker parts when disturbed. A Sarcophagid fly has on one occasion been bred from an adult individual, and both larvae and adults are victimized by hunting wasps. One of the commonest of these is a Sphegid (*Sphex aegyptiacus* ?) which attacks the adults. It may be often seen carrying its helpless prey along the ground by riding on the pronotum of the locust and propelling it by the use of the long hind legs. In some instances Dipterous insects lurk around presumably waiting to lay on the victim. In one case the locust was dug up 12 days after being buried and 135 puparia were extracted from its skeleton. These produced Sarcophagid flies.

A certain number of larvae are caught by the large spiders which inhabit the trees in the autumn.

Birds are probably the chief predators. Desert Babblers (*Argya acaciae*), which live in small companies among desert trees, are responsible for the destruction of large numbers. Other birds that have been observed to prey on either larvae or adults are kites and other species of FALCONIDAE, Hornbills, the Buff-backed Egret (*Ardea ibis*) and the Abdim Bey Stork (*Ciconia abdimii*). The two latter frequently hunt together in companies and destroy large numbers. Moreover they follow the swarms, harrying them constantly.

Man may be mentioned in this connection, in that in certain parts of the country the adult locusts are considered a delicate article of food.

At times when large numbers of adults are frequenting a locality they may be attacked by a bacterial or fungous disease, the nature of which is unknown. Usually individuals thus attacked cease feeding and later drop to the ground and die, no such condition has up to the present been noticed in the case of the larvae.

Migratory Powers of Adults.

The powerful build of the adult locust and its extensive area of wing would incline to the supposition that it is capable of strong and continued flight. Its manner of flight when disturbed is rapid and direct, not slow and erratic as in some of the non-swarming grasshoppers. Dissection, however, has never revealed a distended condition of the air sacs such as occurs in the well-known migratory species which undertake long flights.

That the species is capable of becoming gregarious is evinced by the observed habit of congregating in trees during the winter. Moreover repeated records of flights of swarms have been made by many observers, but how many of these have been verified as being composed of the Tree Locust it is impossible to say. There is evidence of flight taking place during both summer and winter in Darfur and the western portions of the Sudan, and this is probably connected with search for suitable food and ground for laying eggs. Repeatedly observers in these districts have reported flights, sometimes of considerable magnitude, taking place by night. Those observed near the western frontier have always been recorded as moving from the west, but specimens from such flights have seldom been obtained. There is no evidence of any other species moving except by day, and it is probable that all passages by night are those of *A. moestum*.

Vayssière & Mimeur[7] definitely state that in French West Africa this species moves in swarms of considerable size, and M. Vuillet tells me that he has encountered it commonly thus on the Senegal Coast. It is not improbable that further inquiry will

show that flights of some duration are possible from west to east and vice versa, and that this locust is thus truly migrant. At present, however, in the Sudan there is no evidence of anything but short flights in search of food or damp ground for egg-laying.

Effects of Crowding during the Larval Stages and possible Existence of "Phases."

It has been pointed out already in describing the immature stages that there exist two distinct forms of the larva which have been designated "swarming" and "solitary." Under natural conditions the former has been observed only once in the Northern Sudan, when large numbers of eggs were laid in one locality and bands of larvae occupied trees and bushes.

In the southern and western districts this appears to occur more frequently. The "solitary" larva is the one commonly met with at all times.

It is very doubtful if the forms referred to above can be regarded as at all comparable in importance to the phases of the true locusts. Both agree in developing dark pigmented areas in the integument when the larvae are living other than a solitary existence. The adults of *Anacridium* bred from solitary larvae differ slightly from those bred from larvae in bands in being consistently larger. Further than this it is impossible to draw the analogy. The absence of any plasticity in the larva such as characterizes the immature stages of *Locusta migratoria*, and the fact that even the solitary adults can display gregarious habits, indicate that in its mode of life this species does not resemble the true locusts, but rather occupies an intermediate position.

In order to ascertain whether the same type of swarming hopper as that which occurs under the conditions outlined above could be obtained by crowding in cages, rearing experiments were carried out in cages of 3,080 ccm. capacity. Some were reared singly from the first instar (4 days old), and others were crowded up to the number of thirty in a cage.

In no respect were those larvae reared together in cages found to differ from those observed in bands in the field. The production of a yellowing or reddening of the pigment followed on crowding and the appearance of the black markings as previously described. In the solitary individuals the black pigment persisted only in the shape of small isolated dots which did not coalesce, and as a black line on the keel. But by no degree of crowding could any pronounced or general darkening be obtained, and it was invariably found that a dense crowding resulted in a heavy mortality of hoppers.

Damage and Control Methods.

Considerable destruction of trees may be caused by this locust. The occasional defoliation of fruit trees has been mentioned, and more serious damage to gum trees has been reported. The essentially intermittent character of the damage renders this locust a minor pest. Cotton is very occasionally attacked. It is most probable that this locust prefers the leaves of wild trees as food and only resorts to cultivated crops during the season when trees are less attractive. This usually happens about mid-way between the rains. All this is fortunate, since the ordinary methods of destruction are only partly applicable to this locust. The digging up of egg-pods may be resorted to, and the destruction of the very young larvae, while still on or near the ground and soon after their emergence, has been found successful. But once the larvae have ascended trees they cannot be touched except by spraying, which may prove destructive to foliage. Further experiments should be made, however, with other methods and using various dusts in the attempt to discover a satisfactory system for dealing with this pest on the infrequent occasions when it does give cause for some alarm.

A Note on Anacridium moestum moestum, Serv.

The previously known geographical range of this subspecies has been given by Uvarov[4] as "all over South Africa, ranging northwards up to North Uganda (Gondokoro) and Northern Nigeria (Zungeru); it has, however, never been recorded from the forest-regions of Central and West Africa, and it seems that it does not penetrate there." Many more recent records establish its common occurrence in the region of Gondokoro, which is now in Sudan territory. It is known from Kajo-Kaji, Juba, Mongalla and Yei. Further north on the White Nile it has been taken at Renk and Malakal. On the Blue Nile the writer has observed it at Singa and Roseires, and single specimens have been frequently taken during the last two years in the Wad Medani district (Long. 33·32, Lat. 14·24). This appears to be the present northern limit of its range. In the West it has been recorded from Talodi and the Koalib Hills. Comparing this area of distribution with that given for *A. melanorhodon*, it will be seen that the two subspecies overlap throughout a considerable portion of the Sudan. It would appear that *A. moestum* possesses a vast range extending from South Africa to the Sudan, whereas *A. m. melanorhodon* is confined to the drier and semi-arid regions of the north and occupies a narrower belt of country, but one which stretches across the continent.

The two subspecies resemble each other very closely, but Sudan specimens of *A. m. moestum* differ in the following respects: A variegated or marbled effect is given by patches of lighter colour on the head, pronotum, metathoracic segments and hind femora. The chief difference is in the wing, which has a very broad black band extending across more than half of its area. Also the spots in the apical area coalesce to form a continuous irregular line. This difference which is very striking may be easily recognised when the insect is in flight.

The larva has not yet been identified and nothing is known regarding its bionomics.

The Brown-spotted Locust (*Cyrtacanthacris tatarica*, L.).

This species is the less important of the two locusts dealt with here. It merits attention, however, owing to its capacity for sudden and unexpected acceleration in breeding and consequent ability for inflicting damage on the crops among which it occurs.

Its distribution is wide in the Old World. It is said to occur in most parts of Africa and in India, where it occasionally becomes a pest of cotton. It appears to be absent from Egypt.

In the Sudan it has been recorded from as far north as Lat. 18° N., but it probably occurs beyond this line. It is occasionally found in the khors and deltas of the Red Sea Coast. It has been observed as far south as Lat. 4° N. in the Lado and Yei districts. In the north of the country it is chiefly a riverain species, seldom being found far from the river forest strip, except in irrigated districts. Further south its range spreads out east and west. It is not migratory, except in an extremely limited sense when in search of food, nor has it ever been encountered swarming, except on land under crops. Normally it appears to breed only during the rains, and the adults scatter for the winter months. Among crops, however, it can alter its habits somewhat to the extent that some individuals breed throughout the year.

In certain other countries allied species become pests of the first rank, sometimes producing a definite swarming phase, as in the case of the Red Locust (*Nomadacris septemfasciata*, Serv.) of South Africa.

It is unnecessary to mention the complicated synonymy except to point out that the species here dealt with is the same as that referred to by Lefroy (Mem. Dep. Agric. India, i, no. 1. p. 53) as *Acridium acruginosum*, and by Kirby (Fauna Brit. Ind. Acrid. p. 231) as *Cyrtacanthacris ranacea*.

Description of Adult.

The adult, particularly the female, is a robust insect, the male being usually smaller. The average dimensions for both sexes are as follows :—

	mm.	mm.
Total length	57	75
Pronotum	11	14
Tegmen	47	64
Hind femur	25	33

The living insect may be described as predominantly dark chocolate and pale testaceous, with an occasional mixture of reddish brown. Antennae yellow. Head testaceous, with faint and ill-defined dark vertical lines under the eyes and along the frontal carinae. Prosternal spine bent back towards and almost touching the mesosternum. Pronotum with low but distinct keel ; a broad testaceous line extending from the vertex along the carina and suture of the tegmina in a median position ; disc dark reddish-brown, darker posteriorly, with diffuse fine white granules ; lobes pale testaceous above, dark brown below, and pale on the border. Lobes of metanotum pale, and with numerous punctures giving a reticulated appearance. Abdomen entirely pale testaceous. Legs paler, usually slightly infuscated ; hind femora with two dark markings above and with dark ridges on the outer side ; hind tibiae with two rows of pale dark-tipped spines, usually 8 on the inner and 6 on the outer margin. Tegmina pale, but with more than half their area covered by dark brown markings ; subcostal vein reddish, a number of small dark spots behind the costal margin ; lower half of tegmen with about 6 large dark-margined areas, the three-proximal being usually confluent. Wings with a faint yellow suffusion extending from the base outwards.

The male may be distinguished by its smaller size, and by its acutely conical subgenital plate.

The almost entire lack of variation both in structure and colour throughout its range of distribution has been remarked by Uvarov.[4] This also is strikingly noticeable in Sudan specimens. Occasionally an orange colour suffuses the insect, particularly the male, giving it a reddish appearance in contrast to the normal dark brown.

Description of Larval Stages.

There are five normal moults intervening between hatching and adult maturity. The various stages may be distinguished thus :—

First Stage.—Length taken one hour after hatching, 5 mm. Colour light green, thickly sprinkled with small dark rings, from which rise fine whitish hairs, those on the legs being longer ; hind tibiae strongly ridged dorsally, and with a deep furrow on each side of the ridge.

Second Stage.—Average length 24 hours after the moult, 11 mm. Apart from its larger size, this stage is distinguished by the loss of the vermiform appearance of the previous stage and by the more prominent keel on the pronotum, which is marked by a thin white median line. Colour uniformly green, with small faint dark green markings over the entire body surface, which are the dark rings of the first instar become indefinite and diffuse. These rings are more prominent on the hind femora.

Third Stage.—Average length 24 hours after the moult, 14 mm. Green throughout except that a white streak appears on the lateral lobe of the pronotum and bifurcates anteriorly. The white line of the keel is continued over the abdominal segments. Distinct rudimentary tegmina and wings are present.

The above notes refer to the normal green hopper. In cases where more active breeding has taken place, and something resembling swarming has been produced, a condition which has been observed over very restricted areas only, the hopper develops a dark coloration which renders it as distinct from the green form as is the swarming phase of the desert locust from its solitary phase. This dark coloration may begin to appear early after the second moult. During the third stage, however, the dark portions vary greatly both in intensity and area. The pronotum develops dark marks, and the hind femora have spots on the upper surface. Shortly before the third moult, the darker areas on the pronotum have extended and coalesced, and are divided by the white streak which gives the insect a dirty mottled appearance.

Fourth Stage.—The green hopper now may become darker green with a white line on the keel, and on the hind margin of the pronotum. Within the latter line there is a distinct pink area interspersed with black tubercles.

Fifth Stage.—At this stage the hopper becomes very distinctive and easily recognised, though difficult to find owing to its protective colour. In the case of the swarming hopper, during the fourth stage, the colour pattern becomes more defined, and still more so in the fifth stage, when the insect strongly resembles the winged adult in respect of the pronotum and legs. At this stage the head is testaceous, with dark spots near the eyes and median furrow. Antennae yellow. Pronotal lobes with three dark areas, one triangular posteriorly next the keel, one behind the head, and one on the ventral half of the lobe; running between these is the white streak; hind margin and keel whitish; area below rudimentary wings brown mottled with yellowish. Upper surface of the abdomen clearly marked on each tergite with triangular dark marks. Hind femora with three dark spots on the dorsal surface.

Habits of Cyrtacanthacris tatarica.

Observations have been made chiefly in the irrigated cotton-growing district, roughly Lat. 14° N. to 15° N., and adjacent to the Blue Nile. The habits of the insect apart from this region have not been closely studied, but it is known that breeding is confined to the wet season and the adults afterwards scatter to spend the months till the next rain in trees and bushes, feeding sparingly until May, when sexual development begins. It would appear therefore that there is an imaginal diapause of three to six months.

In irrigated areas, on the other hand, breeding continues during the whole year though at a very reduced rate in the winter. Then it is apparently controlled, often to the point of complete inhibition, by low temperatures.

As soon as the temperature begins to rise in March, many females may be found with the sexual organs developing. Pairing also may be noticed. This, however, does not become general until May. In cages, copulation takes place repeatedly over the period during which egg-laying is going on.

The period of time between the fifth moult and the beginning of egg-laying varies considerably, being largely influenced by temperature. Individuals under observation in cages from April till August, that is, during the hottest period of the year, began laying 30 to 40 days after the moult.

The egg-pod is laid in the ground in almost any place which is moist. Soil texture seems to matter little, since oviposition and hatching take place in stiff clay soil and in sand. One individual was observed to oviposit in the hardened cotton soil of a path after a shower of rain. This egg-pod produced hoppers, with only a small mortality, after 25 days. The female does not cover the eggs with soil, but gradually withdrawing the abdomen leaves the froth-plug exposed. There is no evidence of communal egg-laying, and oviposition seems to be scattered through the area affected.

The egg-pod is usually about 9 cm. long, including the froth-plug in the upper passage. The eggs are encased in a covering of cemented soil, but this casing is not so firm as in certain other species, notably *Kraussaria angulifera*, Krauss, which pass through a long diapause in the egg. The value of the hardened covering may be to prevent desiccation and to ensure the escape of the larvae by the only safe route, namely upwards. The number of eggs laid at one time varies. The average number of a large series examined was 180, the minimum and maximum being 160 and 211. Dissection of females has shown from 100 to 150 eggs in about the same stage of development. It would appear that each female can lay up to 1,000 eggs. This may be spread over three months, as in the case of one individual which paired on 6.i.25 and commenced laying on 25.i.25, five egg-packets being laid up to 13.iv.25. During periods of higher temperature egg-laying is more active and at shorter intervals.

The egg when first laid is bright yellow, but within 24 hours turns to a dull brown. Its length is 6 mm. In shape it is slightly curved, and presents a somewhat fibrous appearance at each end. The pattern on the chorion is that of a honeycomb of closely touching hexagonal cells, the walls of which are of equal thickness.

The incubation period in the insectary averages 29 days in February and March, and varies little. In the summer rain season there is an increase in length, with greater variation. Occasionally the period is much longer, 148 days having been recorded at the end of the wet season. This may evince a tendency towards a resting stage in the egg.

The length of the larval life-cycle has been found to vary from 32 to 115 days. There are normally five moults. The fifth larval stage is often prolonged, the period of the moult extending from 15 to 20 days.

Individuals becoming adult in November or December have been noted to pair and lay their first eggs in March, or three months after the fifth moult.

The normally coloured larva is green and seldom noticed among vegetation. It is very active and leaps with agility from the ground when disturbed. It is seldom found on the ground unless wandering in search of food, and usually feeds on tall vegetation.

The young newly-hatched hoppers scatter at once, and do not remain together on the ground as do those of *Schistocerca gregaria*. In cages they climb to the highest points and commence feeding usually within 12 hours of emergence if exposed to full sunlight. Holes are perforated in the leaf lamina. The older larvae feed by preference from the edge of the leaf. Young shoots and leaves are frequently severed by the larvae, which thus give rise to a good deal of " leaf-fall."

The winged insect is not as wary as is the Tree Locust and can be approached easily. It takes to flight quickly, but the movement of flying is a heavy one and never long continued. A continuous flight of more than a few seconds has never been observed, and migration over a long distance is probably never undertaken. The insect is essentially a sedentary one, and when, owing to the drying up or destruction of its food-plants, it is compelled to seek fresh feeding-grounds, it does so in short flights.

Normally, in the northern Sudan, *C. tatarica* is resident throughout the year among the *Acacia* scrub and sparse ground vegetation characteristic of the region. Its constant occurrence, however, in the cotton crop shows that it is capable of passing from its natural habitat and of attacking cultivation. Here, during periods favourable to breeding, there may be a rapid increase in numbers, and a resulting destruction of crops by the hoppers. In the Gezira cotton crop this may occur at two periods of the year. In the spring during April and May a heavy and rapid increase in numbers may take place, due to the occurrence of early showers. The capacity of the female for laying a large number of eggs within a brief space of time easily accounts for the sudden appearance of these bands of hoppers.

In autumn also, during October and November, the young cotton may be attacked by hoppers that are the progeny of females which approach the irrigated land from the surrounding country on the cessation of the rains and the drying up of vegetation. An attack at this time naturally does greater damage than in April, when the crop is nearly picked. The damage consists of defoliation in varying degrees up to an entire stripping of the plant. Green bolls also may be attacked, the boll wall being eaten away and the lint exposed.

On the cutting out of the cotton crop in May the adults, and such hoppers as can arrive there, resort to gardens and trees in proximity to the crop. These are heavily defoliated by the younger adults, which feed voraciously and shortly attain sexual maturity. Pairing goes on and eggs are laid on the advent of the first rains. It is at this time that bands of hoppers may be met with in mass migration in search of food, but it must be remarked that this habit is only occasional and certainly not normal for the species.

The species has a wide range of food-plants, and when pressed for food may become almost omnivorous. Cotton presents its most usual crop food. It has never been noticed attacking any of the Graminaceae, and is not a pest of cereal crops. Among cultivated trees, a marked preference has been noted for members of the genus *Ficus*, but many others can be attacked, with the apparent exception of *Azadirachta indica* (neem).

Coloration of the Hoppers.

Very different though the green and mottled hoppers are in appearance, it cannot be claimed that there is such a fundamental difference between them as exists in the case of *Schistocerca gregaria*. To begin with, both forms can exist together in the field and also in breeding cages, as the following counts of hoppers reared from the eggs show :—

Total Number	Green Hoppers	Per cent.	Mottled Hoppers	Per cent.	Stage of Hoppers
47	10	21	37	79	5th
68	9	13	59	87	4th
136	20	14	116	86	4th
108	6	6	102	94	4th

The facts, however, remain that, on the one hand crowding does produce dark hoppers, and, on the other that a single hopper reared alone never turns dark. So far therefore there is a certain parallelism between the colour forms of this insect and the phases of the true locusts.

In order to ascertain how far the variation of the density of crowding affects the ratio of dark to green hoppers, a series of rearing experiments was performed in which numbers of individuals varying from 1 to 15 together were placed under observation all in cages of the same size. Five counts were made approximately in the middle of each larval stage. It was found that in no case did single larvae turn dark, though green larvae could occur under crowded conditions. The proportion, however, of these diminished greatly under conditions of crowding. Moreover it was observed that the development of the dark pigment took place in the larger number of cases after the 3rd moult.

Control Methods.

No satisfactory method of control has been devised for destroying the hoppers, since they are not attracted by poison bait spread on the ground beneath the plants on which they feed. The adults, however, when collected in trees have been attracted to the ground by poison bran bait thrown out in the evening, and large numbers have been killed in this way. The bait was that used for locust destruction, namely, bran, treacle and arsenite of soda. Birds have been observed to pick up the hoppers when these have been dispersed during the cutting out of the cotton crop.

A Note on Methods of Rearing.

The writer has been led to agree with Faure[1] that the best results are only obtained in breeding-cages out of doors. Even in the hot sunshine of the Sudan most ACRIDIDAE can be reared successfully. Shade should be provided over part of the cage, to which the insects can betake themselves during the heat of the day.

The cage used by the writer resembles that described and figured by Faure. The most suitable dimensions have been found to be 18 ins. by 16 ins. by 16 ins. The lower portion is separate from the upper, but has a raised rim on which the upper half rests. A sliding glass door 5 ins. high is let into one side. This enables the door to be shut back on the arm while the food is being changed. A false bottom is fitted to the lower portion, in which holes are bored for the tubes holding the food-plant and for the glass jars containing soil.

The latter are small battery jars measuring 8 cm. or 4 cm. in diameter. The smaller size has been found large enough and in it eggs are laid freely. The jar is removed with each egg-pod and over it is inverted another jar of similar dimensions held in place by adhesive tape. On hatching the hoppers climb into the upper jar or can be inverted into it, and they can thus easily be transferred to the breeding-cage.

Another receptacle which has been found useful for the rearing of hoppers is a round tin tray measuring 7 ins. in diameter and 1½ ins. in depth. In the centre is a hole with a raised edge for the reception of a tube containing the food in water. The tray is partly filled with sand, and a wire gauze ring is placed round the food-plant in the centre of the tray. The diameter of this ring, which is rendered firm by being soldered to tin round its edges, should be such as to fit accurately the rim of a lamp-glass inverted over it. The lamp-glass is closed above by laying on it an iron ring to which is sewn cotton gauze.

The assistance of the Director of the Imperial Institute of Entomology in arranging for the determination of material is gratefully acknowledged, as is also the continued interest shown by Mr. B. P. Uvarov in the writer's occasional attempts to study the Orthoptera of the Sudan.

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ON EXPERIMENTS IN THE USE OF POISON DUSTS AGAINST ADULT *LOCUSTA MIGRATORIOIDES*, RCH. & FRM., IN THE SUDAN.

By H. H. King, F.L.S., F.E.S.,
and
W. Ruttledge, B.A. (Cantab.).

The Anglo-Egyptian Sudan has, so far as may be ascertained, always been liable to plagues of the migratory locust, *Schistocerca gregaria*, Forsk., generally referred to as the desert locust. In the summer of 1930 in addition to this species swarms of another migratory locust, *Locusta migratorioides*, Rch. & Frm., locally known as the hairy-chested locust, appeared. In most districts natives stated that they had never before seen this second species, but elderly inhabitants of Darfur and northern Kordofan recognised it as having occurred some forty-two years previously for two successive seasons; the first year in large numbers, the second in but small numbers. It was hoped that history would repeat itself and that the hairy-chested locust would be relatively scarce in its second year, but unfortunately this hope has not been realised; *L. migratorioides* was a more serious plague in 1931 than in the preceding year.

The standard method in the Sudan of dealing with the desert locust is that of killing the hoppers by means of poisoned bran bait. The bait is prepared and sun-dried at headquarters (as described in Bull. Ent. Res., xx, pp. 99–101) and issued to the provinces before the hopper season begins. The results obtained from the campaign of 1930 when 1,100 tons of bait were prepared, of which some 660 tons were actually used, demonstrated the possibility of controlling the desert locust, by this means, even in a country such as the Sudan. It was estimated that upwards of 10,000 tons of hoppers, the greater proportion *S. gregaria*, were destroyed, and records indicated that relatively few swarms of this species matured.

When employed against hoppers of *L. migratorioides* the bait has proved effective, although greater care has to be exercised in using it. Hairy-chested hoppers rarely cluster on the bait to gorge and may, when crossing bare spaces, refuse it altogether. They do not, in fact, eat it nearly so readily or so ravenously as do desert hoppers. Experiments with bait containing a higher proportion of arsenic and treacle indicate that such bait is to be recommended in preference to bait containing the normal proportion of these ingredients when this species has to be dealt with; a hopper needs to eat but a very small amount of the more heavily poisoned bait to ingest a lethal dose of arsenic.

There are certain differences in the incidence and habits of these two species of migratory locusts in the Sudan. Flights of *S. gregaria* arrive from the north-east, north and north-west in the early summer and, with the onset of the rains, oviposit in the light sandy soils of the central and northern provinces. The resulting generation leaves at the end of the rainy season, the flights returning in the directions whence their parents came. The flights of *L. migratorioides* arrive in the central and northern provinces at the same time as those of *S. gregaria* but from the west, south and south-east. They will oviposit in almost any type of soil but appear to prefer those of the heavier classes. The return migration of the resulting generation, beginning at the close of the rainy season, is in a general southerly direction and many swarms stay to breed in the southern provinces, particularly it is believed in the marshy regions of the Upper Nile Province.

Notwithstanding that hoppers of *L. migratorioides* may be killed by means of poisoned bait, we are, for reasons enumerated below, led to believe that the control of this species throughout its range by this means alone is unlikely to prove practicable. Where the hoppers occur in arid and semi-arid districts they may be found readily and destroyed, but in tall dense vegetation they escape detection. Further, the transport of bait and working parties through such dense vegetation, over heavy, cracked soil liable to flooding during the rains, presents grave difficulties, and much of the country in which this species breeds during the winter months is very sparsely inhabited by backward tribes. If *L. migratorioides* is to be controlled we are of the opinion that some second method, supplementing that of poisoning hoppers, must be resorted to.

A swarm of desert locusts when in flight usually moves in open formation and is, for all practical purposes, safe from attack. A swarm of hairy-chested locusts, on the other hand, moves in dense, massed formation and should therefore, we believe, prove vulnerable if attacked by means of an effective poison gas or poison dust. A gas would be more expensive and less easy to use than a dust, consequently the experiments described below have been with the latter. Our object was to find a dust which, if delivered from an aeroplane into a swarm of locusts in flight, would cause the deaths of those individuals coming into contact with it.

In 1923, Mally[1] in South Africa when using dry powdered sodium arsenite as a stomach poison against locust hoppers (species not stated) found that it also acted as a contact poison. He records that if the powder were dusted on to the bodies of hoppers, or even only on to the antennae with a hand-bellows, death invariably resulted in a few hours. These results are summarised briefly by Uvarov,[2] who also refers to experiments carried out in the Northern Caucasus by Sviridenko (1926), Korotkikh (1927), Parfentiev (1929) and Vyshelessky (1927), using powdered sodium arsenate against hoppers of *L. migratorioides*. These latter experiments indicated that it was sufficient to place, with a brush, dry sodium arsenate dust on the bodies of hoppers to kill them within twenty-four hours, while analyses of the stomach contents of hoppers so killed revealed no trace of arsenic therein.

Our initial experiments consisted of blowing a cloud of sodium arsenite dust (powdered to pass through a standard 240 sieve) through a cage containing adult *L. migratorioides* and then removing the locusts to a clean cage. The results obtained were irregular, some individuals dying within a few hours with symptoms which suggested paralysis and others being apparently unaffected. It was thought probable that the locusts which died had absorbed arsenic through the integument, so a series of experiments was carried out for the purpose of ascertaining whether arsenic could be absorbed through any part of the integument or only through restricted areas. Sodium arsenite dust was applied, with a brush, to various parts of the anatomy of locusts including the antennae, mesonotum, venter of thorax, auditory organ, abdomen, genitalia and under-sides of tarsi; none of these locusts showed any ill effects within two days. From these results it appeared unlikely that arsenic could have been absorbed through the integument in the initial experiments; the possibility of the dust being inhaled was then investigated.

While we were unable to ascertain the rate at which a locust breathed while flying, it was noted that a locust which had just ceased fluttering breathed at a faster rate than one which had been stationary or relatively quiet for some minutes; if the dust were inhaled this suggested a possible reason for the irregularity of the results obtained from the initial experiments.

The technique of the experiments devised to ascertain whether finely divided particles of sodium arsenite floating in the air were liable to be inhaled by locusts while flying was as follows. The locust was suspended on a thin copper wire, a loop of the wire being placed round the thorax between the first and second pairs of legs.

It was then induced to flutter and while fluttering a moderately dense cloud of the dust (generated by means of a distributor of the type described in Bull. Ent. Res., xvi, pp. 175–176) was blown past it, enveloping it. It was then placed in a clean cage but given no food for several hours to avoid any possibility of dust adhering to its body contaminating the food and so being ingested. Locusts which fluttered in the dust cloud for approximately, but not more than, twenty seconds invariably showed signs of discomfort within half an hour and were usually markedly ill, if not moribund or dead, within two hours; all were dead within twenty-four hours. If the treatment were extended to approximately, but not more than thirty seconds, symptoms of acute discomfort appeared within a few minutes and all were dead within two hours. In the case of locusts which fluttered in the dust cloud for approximately, but not more than, ten seconds no very definite symptoms could be noticed within four hours, but all were dead within forty-eight hours.

A locust when handled frequently regurgitates a drop of dark fluid appearing at the mouth. To exclude the possibility of the dust adhering to the wet mouth-parts and being ingested, locusts were treated in the following manner. A small hole was cut in a sheet of paper, 16 ins. by 13 ins. in size, and the head of the locust pushed through this hole and completely enveloped in cotton lint. Held in this position it would flutter and dust was then blown on the thorax and abdomen. Locusts so treated were placed in cages and kept under close observation; this latter precaution was for the purpose of ascertaining whether they attempted to clean themselves and while so doing carried poison to their mouths. No locust was seen to make any movement liable to result in dust being conveyed to the mouth, and all individuals dusted in this manner died showing symptoms similar to those exhibited by locusts dusted while suspended on a wire.

Locusts which had been dusted in the manner described in the preceding paragraph were killed by means of carbon tetrachloride vapour and their tracheae dissected out; on analysis these tracheae were found to contain appreciable quantities of arsenic.

The symptoms exhibited by locusts, in cages, which have fluttered for a sufficient time in a cloud of sodium arsenite dust suggest paralysis. The power of co-ordinating the movements of the first and second pairs of legs are first lost and the insect pushes itself along on the sternum, by means of the hind legs. It then shows a marked distaste for sunlight, pushing itself into a dark corner where, if undisturbed, it may remain until death supervenes. From twenty to thirty per cent. of the locusts killed in this way died with one or both fore-wings extended at right angles to the body. The time elapsing between the dusting and the onset of the symptoms appears to depend to a certain extent on the temperature; on a warm day (shade temperature over 100° F.), or if exposed to sunlight, the poison takes effect more rapidly than on a cool day or when the locusts are kept in the shade.

Similar experiments, the locusts being suspended on wires, were carried out with other dusts, including native tobacco, sodium fluosilicate and Paris green. In each case the dust used had been passed through a standard 240 sieve. Locusts which had been treated with native tobacco or sodium fluosilicate showed no ill effects within forty-eight hours and at the end of that time were capable of sustained flight. Locusts dusted with Paris green usually showed some signs of discomfort within twenty-four hours and were invariably moribund, if not dead, within forty-eight hours. A single experiment (ten locusts) with arsenious oxide gave results comparable with those obtained with Paris green. It may be noted that while sodium arsenite is highly soluble, both Paris green and arsenious oxide are but slightly soluble in water.

Analysing the results obtained from these experiments we are led to form the following conclusions. If an adult locust (*L. migratorioides*) flies in an atmosphere charged with minute floating particles of sodium arsenite, some of the particles will

reach the tracheae by way of the spiracles. If a sufficient quantity of arsenic reaches the tracheae the result is paralysis followed by death. The rapidity of the action of the arsenic will depend on the solubility of the arsenic salt and to a far less extent on the temperature; this latter factor probably acts indirectly by quickening or retarding the general metabolism of the insect. No evidence was obtained indicating that arsenic in the form of dry sodium arsenite dust is absorbed through the integument.

As regards the possible practical application of these results, as already stated, *L. migratorioides* normally flies in dense massed formation, at no great height from the ground and at no great pace—possibly from ten to fifteen miles an hour. We have consulted an experienced officer of the Royal Air Force, who has seen many flights of this locust, and been assured by him that there should be no insuperable difficulties connected with the discharge from an aeroplane of a cloud of dust (of a density equal to or greater than the dust clouds used in the experiments) into a flight in such a manner that a large proportion of the individuals composing the flight would find themselves in the dust cloud and be unable to emerge in less than twenty seconds. Our experience indicates that a cloud of sodium arsenite dust of a fineness permitting it to pass through a standard 240 sieve behaves as does a cloud of smoke; it floats with the air currents with a general tendency when used in the morning when the sun has warmed the ground, to rise and dissipate. We do not anticipate that a cloud of such dust discharged from an aeroplane will settle in sufficient concentration to be a source of danger to man or the higher animals. Possibly a native eating a number of poisoned locusts would ingest a lethal dose of arsenic, as the dust adheres to the integument of the insects, but it must be remembered that sodium arsenite is bitter to the taste and that consequently a locust dusted with this salt would not be very palatable. Further, natives throughout a district might be warned of the danger of eating locusts when dusting operations were in progress.

We would emphasise that the above are purely laboratory experiments and that we have yet to ascertain whether the results obtained have any practical application. At the same time, in view of the seriousness of the situation as regards this species of locust in certain parts of Africa and the fact that we may be unable to carry out field trials for several months, we believe this early publication to be justified.

In conclusion we would express our indebtedness to Mr. B. W. Whitfield, Government Chemist, for advice on the properties of chemicals, to Mr. H. B. Oakley, Chemist, for analysing the internal organs of locusts for arsenic, and to Mr. F. G. S. Whitfield, Entomologist, for carrying out the dissections necessary.

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A MOSQUITO WITH LARVAL HABITS LIKE *TAENIORHYNCHUS*.

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Mosquito larvae and pupae which get their oxygen from aquatic plants have been seldom met with so far ; all belong to the genus *Taeniorhynchus*. Examining *Pistia* for the latter I found a few times a larva attached to the roots of the plants by means of its modified air-tube. The adults which were bred from these larvae proved to be *Ficalbia* (*Mimomyia*) *hybrida*, Leicester.* The adult has been known for some time, but the larva is new.



Fig. 1. *Ficalbia hybrida*, Leic., hypopygium ; *a*, mesosome.

This is a brownish mosquito of rather small size with a conspicuous light-coloured occiput, metallic bluish iridescence and narrow basal light bands dorsally on the abdomen ; legs unbanded.

Female. *Head* with the *occiput* closely covered throughout with numerous, very light greyish-white, broad flat scales, with pinkish and blue iridescence in certain lights, these along margins of eyes in certain lights quite dark ; in living or freshly killed specimens the occiput is entirely dark ; on the nape a patch of small black upright forked scales ; along margins of eyes a few dark bristles, those projecting in front between the eyes light golden. *Clypeus* dark, with greyish lustre. *Antennae* with the first two segments light brown, remaining segments blackish with grey sheen. Segment 1 with fine short grey hairs and minute dark scales on median surface ; 2 very long, longer than 3 and 4 together, with a single row of long black scales basally all round and a longitudinal row of shorter scales on the outer side. Long and short hairs of joints golden. *Proboscis* dark-scaled with purple iridescence in certain lights, bent and distinctly swollen at outer third, labella large, brownish. Small hairs all over proboscis golden brown. *Palpi* about one-fifth the length of the proboscis, dark-scaled with bluish iridescence.

* Synonyms : *Ludlowia minima*, Ludlow ; *Conopomyia hybrida*, Leicester.

Thorax with the *prothoracic lobes* light brown with dark bristles of moderate size, those in front in a row, those more lateral in a patch and with golden sheen in certain lights. Mesonotum dark, evenly covered with narrow curved, golden brown scales, lying rather flat, particularly so laterally; in certain lights some scales have a greyish hue; on the ante-scutellar space, which has a very small bare area, the scales are rather light brown. Four longitudinal rows of coarse dark bristles on mesonotum, most numerous over roots of wings; in certain lights these bristles have a golden sheen. *Scutellum* with long coarse golden bristles (6 on mid lobe, 5 on each lateral lobe) and long, narrow curved, greyish and creamy-yellow scales, numerous on mid lobe. *Pleurae* golden yellow with greyish sheen; one margin of lower sternopleurae with a row of creamy yellow, rather long, flat scales. On upper sternopleurae a patch of flat creamy-yellow scales, many of which are rather small.

Wings with the fork-cells rather short; dark brown, small, broad scales, lying close to veins, somewhat lighter toward apex of wing.

Legs mostly dark-scaled above, with greenish-blue metallic sheen; femora all with creamy-yellow scales below and partly also in front and behind, basally light-scaled all round. Creamy-yellow scales at tibio-tarsal articulation on all legs; all

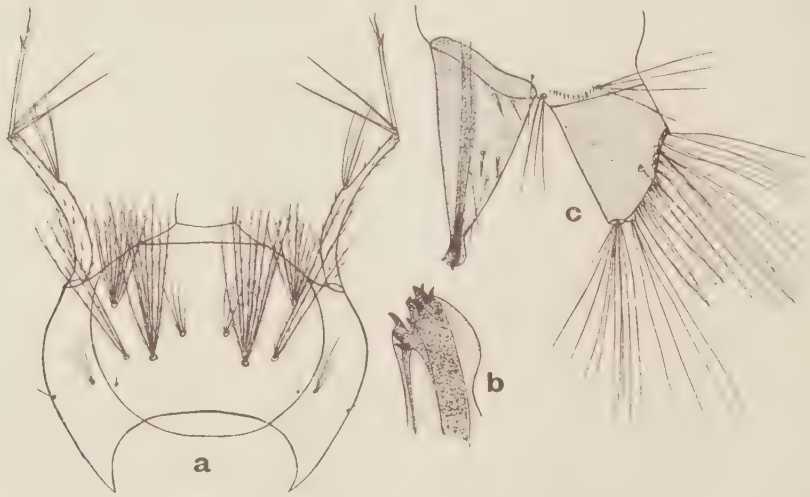


Fig. 2. *Ficalbia hybrida*, Leic., larva: *a*, head; *b*, apex of air-tube; *c*, anal segment.

tibiae with brassy scales beneath; tarsi of mid-legs with brassy sheen beneath, fourth and fifth tarsals on all legs in certain lights with strong brassy lustre on one side.

Abdomen dorsally dark-scaled with violet blue iridescence; very narrow basal bands of brassy scales on segments 2–5; 5–7 with large lateral basal golden-yellow patches; on 4 only a few golden-yellow scales visible laterally at base. Venter mostly covered with greyish scales which have a brassy lustre in certain lights.

Length: body, 3·5 mm.; wing, 2·5 mm.

MALE. *Antennae* not unusually elongated as in the female; all the segments brown with greyish lustre, 2 with a row of long black scales all round. Implantations of hairwhorls black. Long hairs on 2–11 light golden, with greyish tips in certain lights, very long and silky on 7–11; hairs on apical segments short and sparse; 1 large, with sparse fine short hairs on median surface and minute scales. *Proboscis* at basal third and around the bend lighter-scaled than in the female, in certain lights

even creamy-yellow. *Palpi* exceeding the length of the proboscis by the apical segment, which is bent upward at a right angle. On the basal part a rather broad golden band and a long stripe of golden scales just before the bent portion. Extreme tip of palpi with a few greyish-white scales; bent part with stiff moderate golden hairs below. *Legs* with the brassy sheen on the tibiae and tarsi not so distinct as in the female. *Abdomen* with all the segments, except 1, indistinctly basally banded; some of the bands in certain lights hardly visible. The dorsal banding of the abdomen seems to vary in different specimens. Many golden hairs present. Side-pieces with purple and brassy iridescence.

Hypopygium (fig. 1) with the side-pieces long and slender, about three times as long as wide, with simple long slender clasper, bearing a rather long subapical spine. Moderate hairs all over surface of side-pieces. A more or less distinct basal lobe present bearing two long flattened and pointed terminal appendages, two long

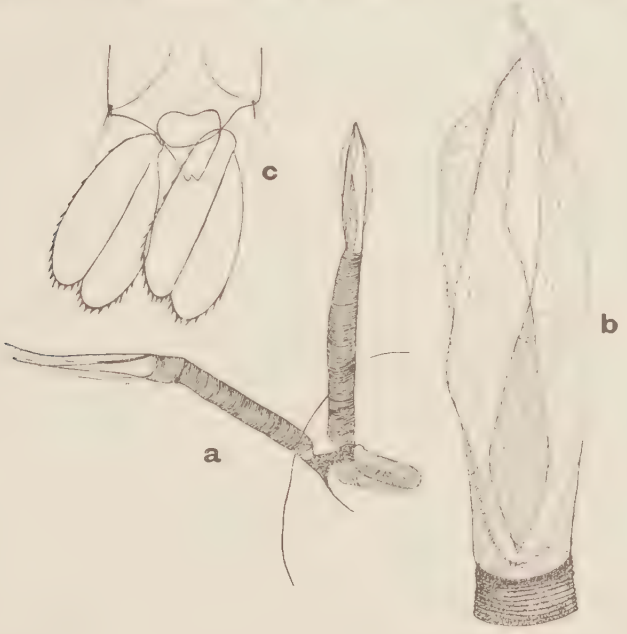


Fig. 3. *Ficalbia hybrida*, Leic., pupa: *a*, breathing trumpets; *b*, outer part of same enlarged; *c*, paddles.

subapical hairs, many moderately long fine hairs, and some minute hairs on apical half. Lobes of the ninth tergites distinct, slender, each lobe with four long coarse hairs. Basal plates and parameres not distinct in our mounts. Mesosome (fig. 1, *a*) very simple, pear-shaped, with the slender part basally and the broad apex slightly excavated. Tenth sternites prominent, two chitinized teeth at apex and three delicate hairs just below.

Length: body about 3·5 mm.; wing more than 2·5 mm.

Larva (fig. 2). Head broader than long. Antennae strongly curved outward, spinose part shorter than head, a four-haired tuft beyond middle; extension of antenna slightly shorter than antenna, no spines present; extension ending in a sharp spine and bearing apically a flat oblong appendage, a hair and a bristle; at the base of the extension two long straight appendages are present, slightly longer than extension. Dorsal head-hairs as follows: Pre-antennal hairs in small 5-haired tufts,

each hair simple ; inner post-antennal hairs in multiple tufts of long feathered hairs ; mid post-antennal hairs in long 3-haired tufts of feathered hairs ; outer post-antennal hairs in multiple tufts of moderately long feathered hairs ; vertical hair small, single ; trans-sutural hairs in small 4-haired tufts of fine hairs ; ocular hair small, single. Comb on the eighth abdominal segment a single row of 12 fine spines. Air-tube less than twice as long as wide, apex modified to pierce tissue of aquatic plants (fig. 2, *b*) ; two pairs of short coarse spines present, more apically a pair of long single hairs. Anal segment ringed by the plate, about as long as wide, a row of sharp spines at hind margin ; anal brush moderate, hairs rather long, lateral hair single, pilose along one side, dorsal hairs in a 4-haired and a multiple tuft, both long. Anal gills narrow, pointed, about as long as anal segment.

Pupa. Breathing trumpets modified at outer two-fifths to pierce tissue of plants (fig. 3, *a*). This outer part is divided in its entire length (fig. 3, *b*). Paddles with distinct sharp spines along edges (fig. 3, *c*). In the living pupa the paddles are bent towards the dorsum of the abdomen, their dorsal surface forming a right angle with it.

Larvae found attached to Pistia in a fresh-water pond, together with *Taeniorhynchus* (*Mansonioides*) *uniformis*, at Batavia, in June 1928 and March 1930.

NOTES ON DUTCH EAST INDIAN MOSQUITOS.

By S. L. Brug,

Geneeskundig Laboratorium, Batavia.

In the collections received during recent years by the Geneeskundig Laboratorium in Batavia there were some specimens that seemed to represent new species. Moreover by rearing isolated larvae the hitherto undescribed larval and pupal stages of some species have been studied. In this paper are also included figures of the hypopygia of some species, already described, but not yet figured by other authors.

I owe many thanks to Dr. F. W. Edwards (British Museum) for the kind help and useful advice he gave me during the preparation of this paper.

The type specimens of the new species and specimens of the hitherto undescribed larvae have been deposited in the British Museum.

Megarhinus aurifluus, Edw., and **Megarhinus kempi,** Edw.

As pointed out by Edwards (Bull. Ent. Res., xvii, p. 114) the larvae of various species of *Megarhinus* are very uniform in structure, whereas the pupal paddles offer characters which may serve to distinguish them. In fig. 1 the pupal paddles of the two above-mentioned species are shown. On comparison with Edwards' figures it is evident that the former species largely resembles *M. quasiferox* and the latter *M. leicesteri*, so far as the paddles are concerned.

M. aurifluus was bred from a pupa found in a pitcher-plant in a swamp in a virgin forest near Dermajoe (Benkulen, Sumatra). The larva of *M. kempi* was found in a bamboo post of a fence in Patjet (Preanger Regentschappen, Java) at about

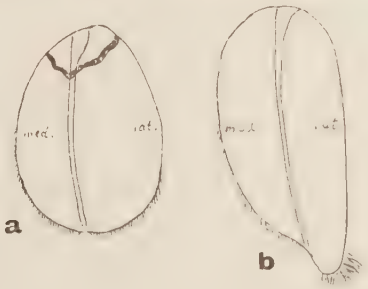


Fig. 1. Pupal paddles of: (*a*) *Megarhinus aurifluus*, Edw.; (*b*) *M. kempi*, Edw.

1,100 m. above sea-level. During the rearing of this larva some observations were made on its behaviour. It was always provided with sufficient larvae of *Aëdes* (*Stegomyia*) *fasciatus*, *Culex brevipalpus* and *Rachionotomyia aranoides*. The spiny larvae of the latter species were devoured just as readily as the smoother looking ones of the other two species, apparently without damaging the *Megarhinus*. When the larva was still small it rejected the heads and the syphons of its victims, afterwards it swallowed them altogether. The larva proved most greedy just before pupation: 10–12 larvae a day were eaten during the last four days, though previously never more than four a day. Anopheline larvae were eaten just as readily as Culicines.

Uranotaenia macfarlanei, Edw.

Description of larva (fig. 2). Head rather broad, with the usual two pairs of thick spiny hairs. Mental plate a little bit broader than long, bearing 13 teeth. Antenna with a simple short hair near its base ; terminal bristles shorter than half the antenna. Comb on the eighth segment consisting of about 10 smooth, pointed teeth. Siphon cylindrical, index 4, pecten teeth about 14, densely fringed, siphon tuft beyond the middle with about 9 branches. Inner dorsal hair of anal segment three-branched, outer one two-branched ; lateral hair moderately long, six-branched. Gills shorter than anal segment.

Described from three larval skins and two larvae, found in a small pool with dirty water (rotten leaves) near Dago (Preanger Regentschappen, Java) at about 900 m. above sea-level.

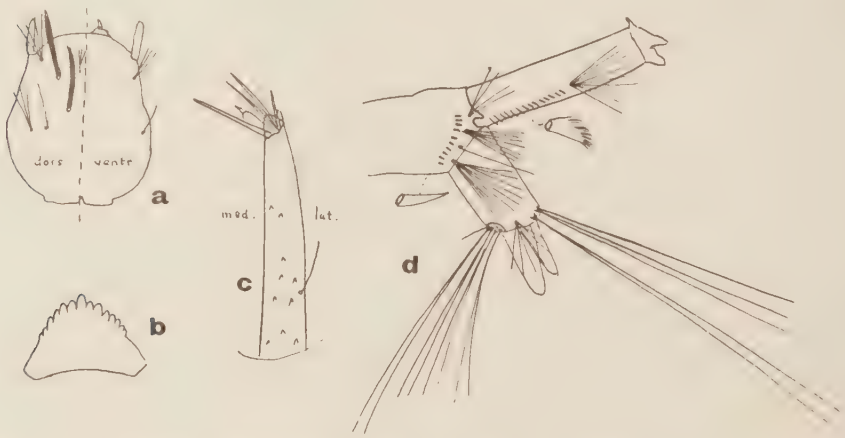


Fig. 2. *Uranotaenia macfarlanei,* Edw. : *a,* head ; *b,* mental plate ; *c,* antenna ; *d,* posterior end of larva.

Rachionotomyia proxima, Edw.

Description of larva (fig. 3). Head roundish. Antennae small, bent, with the convexity towards the medial side ; in addition to the apical adornment a very small simple hair near the tip. Mental plate narrow, with 13 teeth, mid one very large, the others about equal. Comb teeth of eighth segment in one straight row, very slender, the tip blunt and slightly fringed, the teeth not on a chitinised plate, 10–15 in number ; in one larva there were 14 teeth on one side and 22 on the other. Siphon : index 3–3½, pecten of 3–5 slender sharp teeth on the apical part of the siphon (in fig. 3 siphon hairs and pecten teeth of both sides are drawn) ; hairs on ventral side two-branched, those on lateral and dorsal sides simple or two-branched and irregularly distributed. Anal saddle large ; inner dorsal hair on anal segment 4–6 branches, moderately long, outer dorsal hair simple, very long ; lateral hair long and simple or with 2–5 branches. Anal fan consisting of one 3–5 branched hair only.

The terminal appendages of the pupal abdomen are shown in fig. 3.

Description from 3 skins of larvae and pupae, collected in a rot-hole of a tree in Dermajoe (Benkulen, Sumatra, at about sea-level) and two others found in bamboo stumps in Patjet (Preanger Regentschappen, Java, 1,100 m.).

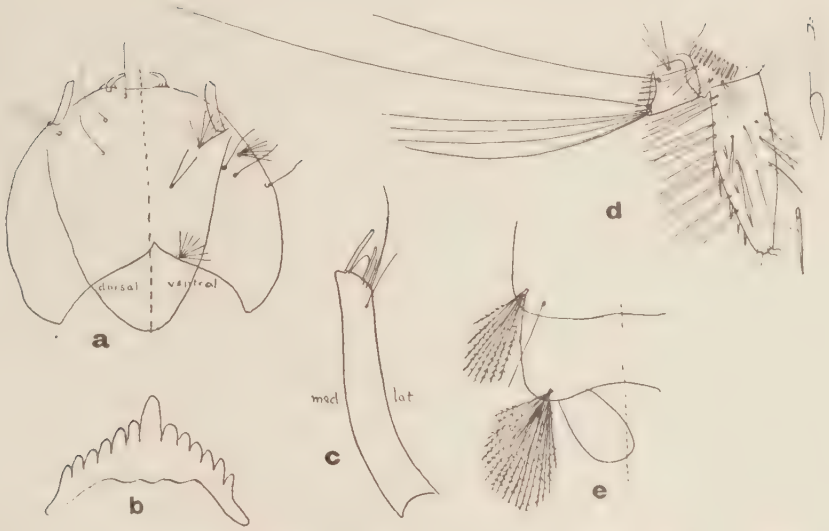


Fig. 3. *Rachionotomyia proxima*, Edw.: *a*, head; *b*, mental plate; *c*, antenna; *d*, posterior end of larva; *e*, posterior end of pupa.

Heizmannia aurea, sp. n.

Female. Vertex with flat, pale brown scales, showing a metallic green lustre in some lights, or appearing silvery white in another position. Proboscis 7 times as long as palpi, longer than the fore femur and shorter than the abdomen. Palpi, clypeus, tori and proboscis brown, the rest of the antennae missing, proboscis somewhat paler at the base than toward the tip.

Prothoracic lobes almost touching, provided with flat scales, which show the same colours as those of the vertex. Mesonotum, scutellum and proepimeron with pale brown, flat scales, metallic green in some lights, but in no position silvery. Remaining part of pleurae with patches of flat scales, silvery in any position. Metanotum with a tuft of brown hairs on the posterior end. Wings with very narrow brown scales; first fork-cell 8–5 times as long as its stem, second one 7–4 times as long, the base of the former nearer the base of the wing. Legs brown with coppery hue, outer side of hind femur with a pale yellow metallic lustre in some positions.

Abdominal tergites brown, the first one with a green metallic lustre, the second, third and fourth metallic blue, and the remaining one with a purple gloss. On the tergites 1–6 there are white basal lateral spots. Sternites 1 and 2 invisible; 3–5 basally white, apically brown; 6–8 all brown.

Description from one female captured by Dr. Lach de Bère in Halmaheira (Moluccas).

This *Heizmannia* can be readily distinguished from any other species of the genus by its general pale brown appearance.

Aëdes (Finlaya) derooki, sp. n.

Female. Vertex with dark brown flat scales and forked scales of the same colour; anteriorly a median patch of silvery-white curved scales. Proboscis five times as long as palpi, longer than fore femora and shorter than abdomen. Palpi, proboscis and antennae dark brown.

Mesonotum with small, brown, curved scales and a median stripe of small silvery-white, curved ones; the stripe occupying one-fourth the width of the mesonotum, anteriorly slightly narrower, beginning just behind the anterior border and ending about level with the wing-bases. Scutellum with small, dark brown, curved scales on all the lobes; at the tip of the mid lobe however there are some sparse golden-brown ones. Prothoracic lobes with many dark brown hairs. Proepimera with small, dark brown, curved scales on the upper half. Remainder of pleurae with some dirty yellowish-brown, flat scales and very hairy, but no hairs on the lower half of the mesepimeron. Wings with dark brown scales, the outstanding ones narrow. First fork-cell about as long as its stem, second 1·5 times as long, the base of the latter much nearer the wing-base. Legs mostly dark brown; inner sides of femora dirty yellowish; white basal bands on the first and second tarsals of the fore legs, on the first, second and third tarsals of the mid legs, and on all the tarsals of the hind legs; those on tarsals 1–4 of the hind legs very broad; white knee-spots on mid and hind femora.

Abdominal tergites dark brown; on tergites 2–6 a pair of paramedian, dirty yellow spots between the base and the apex and dirty whitish, basal lateral spots; the latter ventrally slightly removed from the bases of the tergites.

Description from two females reared by Dr. de Rook from larvae captured in rock pools in a river-bed in Ternate (Moluccas).

This species comes in the group of Australian *Finlaya* with a broad median stripe of white scales on the front half of the mesonotum (Edwards, Bull. Ent. Res., xiv, p. 380) near to *A.* (*F.*) *albitarsis*, differing from it in having very small scales on the thorax, not 'hair-like' ones, in having no white scales on the prothoracic lobes, no bands on the abdomen, and the fifth hind tarsal banded.

Aëdes (Finlaya) argenteitarsis, sp. n.

Female. Vertex with flat black scales and a narrow rhomboidal patch of white curved scales, extending between the eyes. Laterally a patch of flat white scales. Proboscis long, 1·5 times as long as the fore femur, about as long as the abdomen, 5·5 times as long as the palpi. Proboscis and palpi dark brown.

Mesonotum with small, dark brown, curved scales and a median stripe of small, white, curved scales, about one-fifth as broad as the mesonotum and extending from near the anterior border to a line connecting the wing-bases. This stripe gradually narrows posteriorly. Scutellum with small white curved scales on the mid lobe and large black curved ones on the lateral lobes. Prothoracic lobes with small white flat scales on the posterior face. Proepimeron with a small patch of white flat scales. A line of flat white scales from the base of the wing extending forward till half-way to the posterior border of the proepimeron. Wings with dark brown scales, the outstanding ones narrow. First fork-cell about twice as long as its stem, second 1·5 times as long; base of the former nearer the wing-base. Legs dark brown. Basal white banding on the first and second tarsal segments of the fore leg; on the mid leg, white bands at the apex of the femur and at the base of the first tarsal segment, and a white spot at the base of the second one; hind leg with a white knee-spot on the femur and all the tarsal segments with broad white basal bands, those on the third to fifth segments occupying more than half the length of the segment.

Abdomen dark brown, with a silvery-white lateral band for the whole length of the first tergite and lateral basal spots on the second to sixth tergites. Sternites 2–7 dark brown with silvery-white lateral basal spots.

Described from one female, captured by Dr. H. de Rook near Upper Digoel River (South New Guinea).

This mosquito also resembles *A.* (*F.*) *albitarsis* but can be distinguished from it *inter alia* by having an unbanded abdomen, a white mid lobe of the scutellum and a largely white fifth tarsal segment on the hind leg. From *A.* (*F.*) *derooki* it differs by having the white stripe on the mesonotum less broad, by the white mid lobe of the scutellum, by the absence of yellow submedian spots on the abdominal tergites, and by the broader banding of the fifth hind tarsal segment.

Aedes (Ochlerotatus) purpuraceus, sp. n.

Female. Vertex with dark integument and mostly creamy-yellow scales, broad and curved in the middle, flat at the sides; a border of smaller curved ones along the eyes; small curved scales on the occiput, where there are moreover dark brown, forked scales. Proboscis 4 times as long as the palpi, somewhat longer than the fore femur and shorter than the abdomen. Palpi and proboscis dark brown. Antennae dark brown, tori ochraceous.

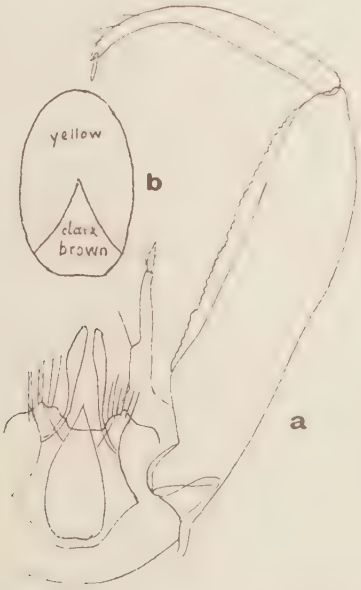


Fig. 4. *Aëdes* (*Ochlerotatus*) *purpuraceus,* sp. n.: *a,* hypopygium; *b,* scaling of mesonotum.

Prothoracic lobes with many creamy-yellow, lanceolate scales. Mesonotum with creamy-yellow, narrow curved scales but for a large triangle with its apex at about the middle of the scutum and its base formed by the posterior border, which is covered by dark brown scales (fig. 4, *b*). Scutellum with few dark brown, narrow curved scales on the mid lobe and no scales on the lateral lobes. Pleurae with many broad, flat, creamy scales and a patch of creamy, narrow curved scales on the lower part of the sternopleura. Mesepimeron without bristles but with some white soft hairs on the upper part and in the middle. Wing veins thickly clothed with moderately broad, dark brown scales, especially the branches of the second longitudinal vein. Wing membrane pale brown. First fork cell 4–3 times as long as its stem, second one 5–3 times as long; the base of the latter nearer the wing-base. Legs dark brown, except the inner sides of the femora, these being clothed with creamy-yellow scales.

The first abdominal tergite with greyish brown integument, hairy and with a median patch of black scales; other tergites metallic violet with creamy-yellow, basal, lateral spots. Sternites creamy yellow basally, dark brown apically.

Male. Antennae plumose. Palpi brown; the apical and subapical segments, together with the tip of the long segment, very hairy. The palpi exceed the proboscis in length by about $1\frac{1}{2}$ segments. Colour markings as in the female. Hypopygium: fig. 4.

Described from two males and a female captured by Dr. H. de Rook near Upper Digoel River (South New Guinea).

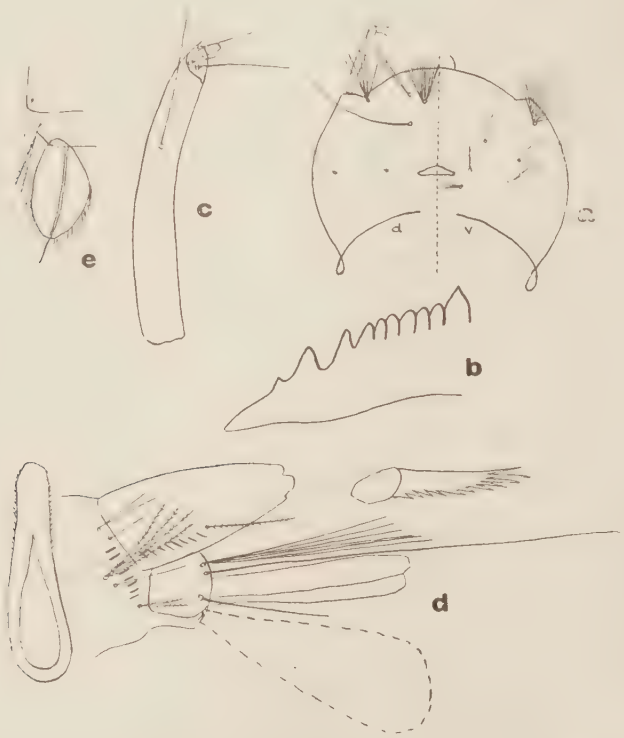


Fig. 5. *Aëdes (Skusea) iyengari*, Edw.: *a*, head; *b*, mental plate; *c*, antenna; *d*, posterior end of larva; *e*, posterior end of pupa.

Aëdes (Skusea) iyengari, Edw.

Description of larva.—Head rounded. Pre-antennal hair and outer post-antennal hair many-branched, mid post-antennal hair bifid, inner one long and simple. Occipital hairs small and simple. Antennae moderately long, curved inward, with a simple hair implanted beyond the middle, exceeding the apex of the antenna by about a third of its length. Mental plate narrow, with 17 teeth, the mid one and two lateral ones on each side larger than the others.

Comb on eighth segment formed by a single row of 7–10 scales with a blunt apex and very scantily fringed. Siphon: index 2–$2\frac{1}{2}$, conical, with rounded sides; a simple fringed hair at about the middle of its length. Pecten consisting of 7–14 barbed teeth. Eighth segment with the inner dorsal hair moderately long, 5–6 branched;

the outer one long and simple ; the lateral hair simple and twice as long as the segment. Anal gills cylindrical, about as long as the siphon (fig. 5).

The terminal appendages of the pupa are also depicted in fig 5.

Described from four larval and four pupal skins, collected from bamboo stumps in Meester Cornelis (near Batavia, Java), about sea-level.

Aëdes (Aëdes) dux, Dyar.

This mosquito and its hypopygium were described by Dyar (Ins. Ins. Mens, xiii, p. 81) but no drawing of the hypopygium was published. I have been able to compare the hypopygium of a specimen caught on my writing desk in Batavia with



Fig. 6. *Aëdes dux*, Dyar : hypopygium.

a drawing which Mr. Dyar had sent to Dr. Edwards and to convince myself of their identity. The former is depicted in fig. 6. It may be noted that the hypopygium is almost wholly covered by the 7th and the 8th abdominal segments, so that externally the side-pieces cannot be seen, only the tips of the claspers being visible.

Aëdes (Aëdes) macrodixoa, Dyar.

A male specimen of this species was captured by Dr. de Rook near Upper Digoel River (South New Guinea). Its hypopygium proved to tally with a drawing Mr. Dyar also sent to Dr. Edwards (fig. 7).

Aëdes (Aedes) funereus, Theo.

The hypopygium of this mosquito has been described by Edwards (Bull. Ent. Res., xii, p. 76) ; it is figured here for the first time (fig. 8).

Aëdes (Leptosomatomyia) medialis, sp. n.

Female. Vertex densely clothed in the middle with golden yellow, narrow curved scales, the posterior two-thirds of this area with grey forked ones also ; laterally velvet-black, flat scales, then a narrow band of white flat scales and ventrally black

scales again. Antennae dark brown, tori ochraceous, the latter with some flat, small, golden-yellow scales. Proboscis and palpi dark brown ; the former 5·5 times as long as the latter.

Prothoracic lobes with golden-yellow, curved scales. Mesonotum with small, dark brown, narrow curved scales and golden-yellow ones ; the latter form a definite stripe at the anterior and lateral borders, and a median stripe, the posterior part of the latter being less definite, because it is intermixed with many dark brown scales. On the remaining part of the mesonotum there are a few isolated yellow scales amongst the brown ones. The anterior border of the mid lobe of the scutellum is

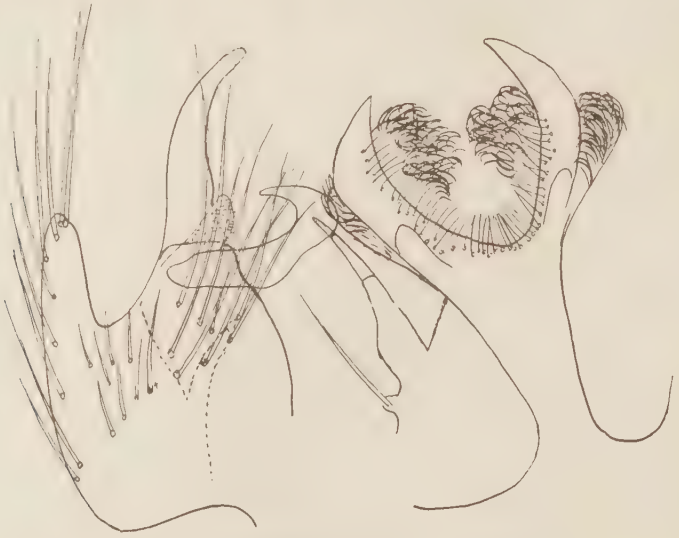


Fig. 7. *Aëdes macrodixoa*, Dyar : hypopygium.



Fig. 8. *Aëdes funereus*, Theo. : hypopygium.

clothed with golden-yellow, curved scales, the remainder of the scutellum with brownish black, curved scales. Pleural integument dark brown, with patches of creamy-white scales. One of the latter is situated on the mesepimeron and is V-shaped, the open side of the V being directed backward. Wing scales dark brown with a beautiful pale brown gloss in some lights. First fork-cell twice as long as its stem, second 1·5 times as long ; the bases of the fork-cells level. Legs dark brown with yellow and white ornamentation ; fore femur narrowly banded with yellow near its apex, at about 1/5 of its length, the band interrupted by some dark scales ; basal half on the inner side creamy yellow, a row of scattered pale scales toward the apex.

Mid femur similarly but more distinctly banded, inner side creamy yellow at the base, with scattered pale scales apically. Hind femur as the mid femur, but with an additional patch of yellow scales at the outer side basally occupying about 3/5 of the femur. Tibiae dark brown. Tarsi with white basal bands, fore ones on the first three segments, mid ones on the first four segments, and hind ones on all the segments.

Abdominal tergites dark brown with a medial, basal, creamy patch on each of them and lateral spots of the same colour; these lateral spots begin at the basal ventral corner of each tergite, continue along the ventral border until the apex and then bend dorsally for a little distance along the apical border.

Male. Differs from the female in the following respects: Proboscis hardly four times as long as the palpi. Antennae plumose. Median stripe of mesonotum less distinct. Fore femur with a patch of pale scales instead of a subapical band. Tibiae of mid and hind legs basally banded. All the tarsal segments of all the legs basally



Fig. 9. *Aëdes* (*Leptosomatomyia*) *medialis*, sp. n.: side-piece with clasper and mesosome.

banded. On the abdominal tergites the median, basal creamy patches extend over more than half the length of the tergites. The lateral spots on the tergites are more obliquely (less angularly) produced toward the apical borders of the tergites than in the female. The first fork-cell is 1·6 times as long as its stem, the second 1·5 times as long, the bases level.

Hypopygium: Side-piece with a sub-basal tuft of broad flattened hairs on the inner side (fig. 9).

Described from two females and one male reared from larvae, living in pitcher-plants and collected near Upper Digoel River (South New Guinea) by Dr. H. de Rook.

Culex (Lophoceratomyia) digoelensis, sp. n.

Female. Vertex with black flat scales and some black, upright forked ones. Proboscis, palpi and antennae black. Proboscis 7 times as long as the palpi, longer than the fore femur and shorter than the abdomen.

Mesonotal integument black, with small, brown, curved scales. Scutellum with similar scales. Pleurae all black. Wings with dark brown scales; first fork-cell 2·5 times as long as its stem, second a little longer than its stem, the base of the first one much nearer the base of the wing.

Abdomen and legs with dark brown scales only.

Male. The colour markings as in the female. Palpi: length of the basal joint one-third of that of the proboscis, long joint two-thirds as long, apical and subapical joints together two-sevenths as long as the proboscis. Antennal ornamentation as

in *C.* (*L.*) *infantulus*. Hypopygium differing from that of *C.* (*L.*) *infantulus* as described by Edwards (Ind. Jl. Med. Res., x, 1921, p. 287) by having tubercular, not spinose, lobes on the mesosome, with rounded tips; moreover the tenth sternite has no membranous projection, but one stout spine, three smaller, but well developed spines and three minor spines; the bases of the lobes of the mesosome with a medially directed hook.

A male and a female of this species were caught by Dr. H. de Rook near Upper Digoel River (South New Guinea).

Culex (C.) papuensis, Tayl., and **C. (C.) squamosus,** Tayl.

The hypopygia of these species are figured here for the first time (fig. 10).

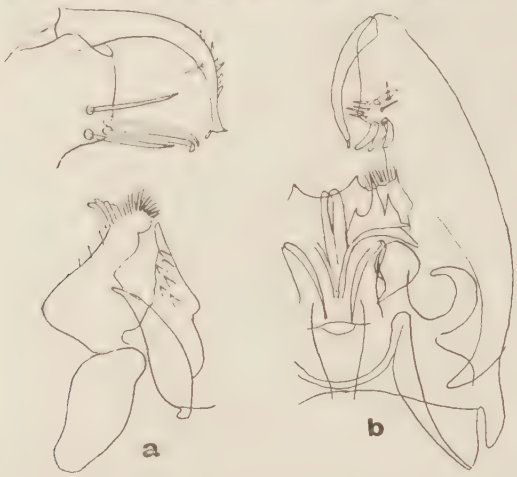


Fig. 10. (*a*) *Culex papuensis*, Tayl., tip of side-piece with clasper and mesosome; (*b*) *C. squamosus*, Tayl., hypopygium.

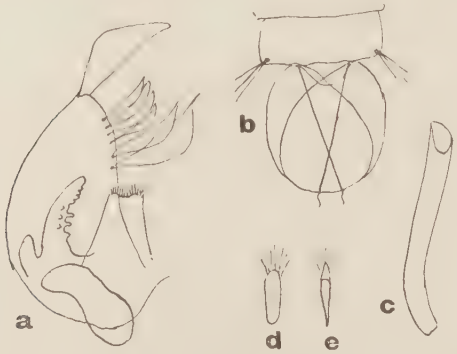


Fig. 11. *Culex castrensis* var. *foliatus*, n.; *a*, hypopygium; *b*, posterior end of pupa; *c*, trumpet; *d*, scale on 8th segment of larva; *e*, scale on 8th segment of larva of *C. castrensis* according to Senior-White.

Culex (C.) castrensis var. **foliatus,** nov.

In external appearance this variety cannot be distinguished from *C.* (*C.*) *castrensis*, Edw. The male genitalia differ from those of the latter species in that the side-pieces are adorned with six fairly broad leaves instead of with two rods and four

bristles. Instead of the small spines on the lobes of the mesosome of *C. castrensis* the variety *foliatus* has fairly large blunt processes (fig. 11).

The larva of *C. castrensis* has been described by Senior-White (Spolia Zeylanica, xiv, p. 71). That of var. *foliatus* agrees closely with this description, only the scales on the 8th abdominal segment are broader (fig. 11, *d*, *e*). For the pupal trumpet and the paddle see also fig. 11.

Described from two males and one female with two larval and two pupal skins, all from a small pool with clear water near Bandoeng (Preanger Regentschappen, Java) at about 900 m. above sea-level.

LYGUS SIMONYI, REUT. (HEM. CAPSID.), A PEST OF COFFEE IN KENYA COLONY.

By Richard H. Le Pelley, Ph.D.,

Entomologist in the Department of Agriculture, Kenya Colony.

(Plate VII.)

Early in 1930 a very serious condition of the young coffee flower-buds was noticed in the Kiambu district of Kenya. The flower "spikes" at an early stage of their growth turned black, failed to open, and did not set fruit. It is not unusual for a small proportion of the flowers of coffee to abort, but in March and April 1930, when a heavy flowering was expected, and where an early examination of the trees showed that a wealth of young flower-buds was present, the percentage of flowers that turned black and aborted in the "spike" stage was so high that the condition was at once recognised to be very serious.

Almost immediately after these observations were made in the Kiambu district, a report was received of a similar and strikingly serious condition at Nyeri, another coffee-growing district about 90 miles from Kiambu. And later in the year it was reported from other coffee-growing districts in the country.

At first no adequate explanation of this affection of the buds could be given; it was generally considered that it might be due to an abnormal physiological condition of the tree owing possibly to a rainfall rather more heavy than usual in the previous twelve months. Some planters stated that they had seen this flower-bud blackening previously, at the higher altitudes in which coffee is grown, and considered that it might be due to cold or lack of adequate sunshine.

On the estate where this was first noticed in 1930, and where the condition was serious throughout the year, however, a Capsid bug was present in large numbers on the trees, which was later identified as *Lygus simonyi*, Reut.

It is interesting to notice that a similar condition had been recorded in Uganda, where the Entomologist reported as follows[1]:—

"Abortion of Coffee Flower Buds—

". . . Considerable time has been spent on the investigation of this problem with the object of determining what insects, if any, were involved. Some five species of Capsidae . . . have been found sucking flower buds in the affected areas, but in every instance the insects were remarkably scarce, and it seems unlikely that they could be responsible for more than a negligible amount of damage. . . .

"The opinion is generally held that the cause of the trouble is the abnormal rainfall. Lower temperatures of air and soil, reduced sunshine, waterlogging of the soil, and high humidity of the atmosphere may all have adverse effects on flower development."

And in a later report[2]:—

"Of the five species of Capsidae observed attacking coffee flower buds only one, *Volumnus obscurus*, Popp., has yet been identified. An attempt was made to test damage by such Capsids but no positive result was obtained; the bugs died within a few days and aborted flowers occurred equally on exposed and protected branches."

Survey of Flower-bud Damage.

In visits to estates in different districts, estimates of the amount of "black-blossom" and of the number of bugs were made, and the estates roughly classified in three groups (A, B, C) in respect of each condition. Thus in respect of flower abortion "A" signified a very great loss due to this cause, "B" a moderate loss, and "C" a slight loss only: and in respect of the number of bugs "A" signified a very large number (in one estate labelled "A" counts showed the average number of bugs to a tree to be about 200), "B" a moderate number (not more than 50 to a tree), and "C" a small number (not more than 3 or 4 to a tree).

In the case of each district in the table, column (1) gives the condition of flower abortion, and column (2) the condition in respect of the number of bugs :—

	Kiambu		Nyeri		Thika		Ruiru		Nairobi	
	(1)	(2)	(1)	(2)	(1)	(2)	(1)	(2)	(1)	(2)
Estate 1	A	A	B	B	A	A	C	C	C	C
,, 2	C	C	A	A	C	C	C	C	B	B
,, 3	B	B	C	C	C	C	C	C	—	—
,, 4	C	C	No abortion	Bugs absent	C	C	—	—	—	—
,, 5	B	B	B	B	C	C	—	—	—	—
,, 6	C	C	—	—	C	C	—	—	—	—
,, 7	C	C	—	—	No abortion	Bugs absent	—	—	—	—
,, 8	C	C	—	—	—	—	—	—	—	—
,, 9	C	C	—	—	—	—	—	—	—	—
,, 10	C	C	—	—	—	—	—	—	—	—
,, 11	C	C	—	—	—	—	—	—	—	—
,, 12	C	C	—	—	—	—	—	—	—	—
,, 13	C	C	—	—	—	—	—	—	—	—
,, 14	C	C	—	—	—	—	—	—	—	—

The table shows not only that the direct correlation between the number of bugs and amount of damage was everywhere maintained, but also the varying condition in both these respects of different estates in districts differing in altitude, rainfall, hours of sunshine and other climatic factors. On this account it seemed unlikely that climatic conditions alone could be responsible for the failure of the flowers. Despite the fact that the general opinion among experienced coffee-planters and authorities on coffee-growing in Kenya was that the bug was not the cause of this abnormal condition of the buds, and that entomological observations in Uganda seemed to show that none of the five Capsids present was connected with a similar condition in that country, after the first observations on a few estates the writer decided to begin experiments to determine whether or not *Lygus simonyi* could cause the flower abortion.

Experimental Production of Flower-abortion.

A large number of experiments were made by introducing bugs to coffee shoots with young flower-buds, and protecting similar shoots from them. In the first series a cloth sleeve was placed over a primary branch of a coffee tree and a number of bugs were placed in it, the control being a similar sleeve without bugs on a similar

primary of the same tree. These shoots were examined and the result recorded from 1 week to 3 weeks after the start of the experiment :—

Result.

Sleeve 1 with bugs ... ... Black and unopened flower " spike."
C1 without bugs ... Green and healthy flower " spike."
Sleeve 2 with bugs ... ... All buds black, or had dropped from tree.
C2 without bugs ... A few buds black, the majority green and healthy.
Sleeve 3 with bugs ... ... All buds black, no flowers.
C3 without bugs ... Nodes 1–10 all buds healthy, except one black bud in node 7. Flowers at three nodes.

In one trial two small wire gauze cages were fitted, each over two nodes, and bugs introduced into one :—

Result.

Gauze cage 4 with bugs ... Buds black, no flowers.
C4 without bugs Fully opened flowers from both nodes.

In another experiment a coffee tree was enclosed in a wooden cage with muslin sides. Two primaries were sleeved to protect them from bugs which were introduced to the cage. This was started on 28th May :—

Result.

Cage 1, with bugs—
11th June ... ... Many black buds, no flowers.
9th July ... ... Nearly all buds black, no flowers.
7th October ... ... Cage removed. Not one flower opened during the whole course of the experiment and consequently no fruit set.

Two sleeves (in cage 1) without bugs—
11th June ... ... Healthy buds in one sleeve, healthy buds and flowers in the other.
9th July ... ... Healthy buds and flowers in both sleeves.
7th October ... ... Sleeves removed. In both sleeves fruit had set normally and was partly grown.

Another tree was placed in a similar cage and in this case four shoots were sleeved and bugs introduced into two of them, the other sleeved shoots and the tree being protected from bugs. This was started on 21st June.

Result.

Cage 2, without bugs—
15th September ... Nearly all buds healthy and likely to blossom soon.
7th October ... ... The tree has flowered normally and fruit has set. There are a few black buds.

Two sleeves (in cage 2) with bugs—
15th September ... Many buds black.
7th October ... ... Nearly all buds black or have dropped. In the upper part of one sleeve two flowers were produced, and in the upper part of the other six flowers were produced.

Two sleeves (in cage 2) without bugs—
15th September ... Buds green and near blossoming.
7th October ... ... All buds healthy, normal flowering and set of fruit in both.

In this case 20 bugs were introduced into each of the two sleeves on 21st June, and at this time only the lower buds on the sleeves were at a stage likely to receive damage. Two weeks was the longest time the bugs were found to remain alive in

the sleeves, and this probably accounts for the flowering at the distal end of the sleeved shoot. It will be seen also that there were a few black buds on this tree. In this work there was constantly the difficulty that *Lygus* was present, sometimes in large numbers, throughout the district where the experiments had to be made, and a small number of buds, however healthy the shoots may have looked when chosen, were almost certain to have been damaged naturally by the Capsid. Figures given later will show that the number of buds damaged experimentally is significantly higher than the number turning black naturally in the field.

Two wood and gauze cages with glass tops, so that the condition of the buds could be observed throughout, were used in another experiment. Into one a shoot



Fig. 1. *Lygus simonyi*, Reut. : adult (x about 11).

on the tree was placed through a sleeve and bugs were introduced ; into the other a shoot was similarly placed without bugs. All the buds appeared healthy on this date, 28th August. On 14th September their condition was :—

Cage with bugs ...	... Buds black 70, buds green 22.
Cage without bugs	... Buds black 3, buds green 74.

Later it was seen that no fruit set in the cage with bugs, while fruit set normally in the other.

Further experiments were made with cut shoots. Shoots on which all the buds appeared healthy were cut, and a number of buds were removed at random from different nodes and examined in detail with a binocular microscope. The number of buds in which any of the stamens showed spotting was recorded. (It will be shown later that the first effect of the feeding of the bug is to cause a spotting of the stamens.) The shoots with the buds that remained on them were then fed to bugs or kept as controls.

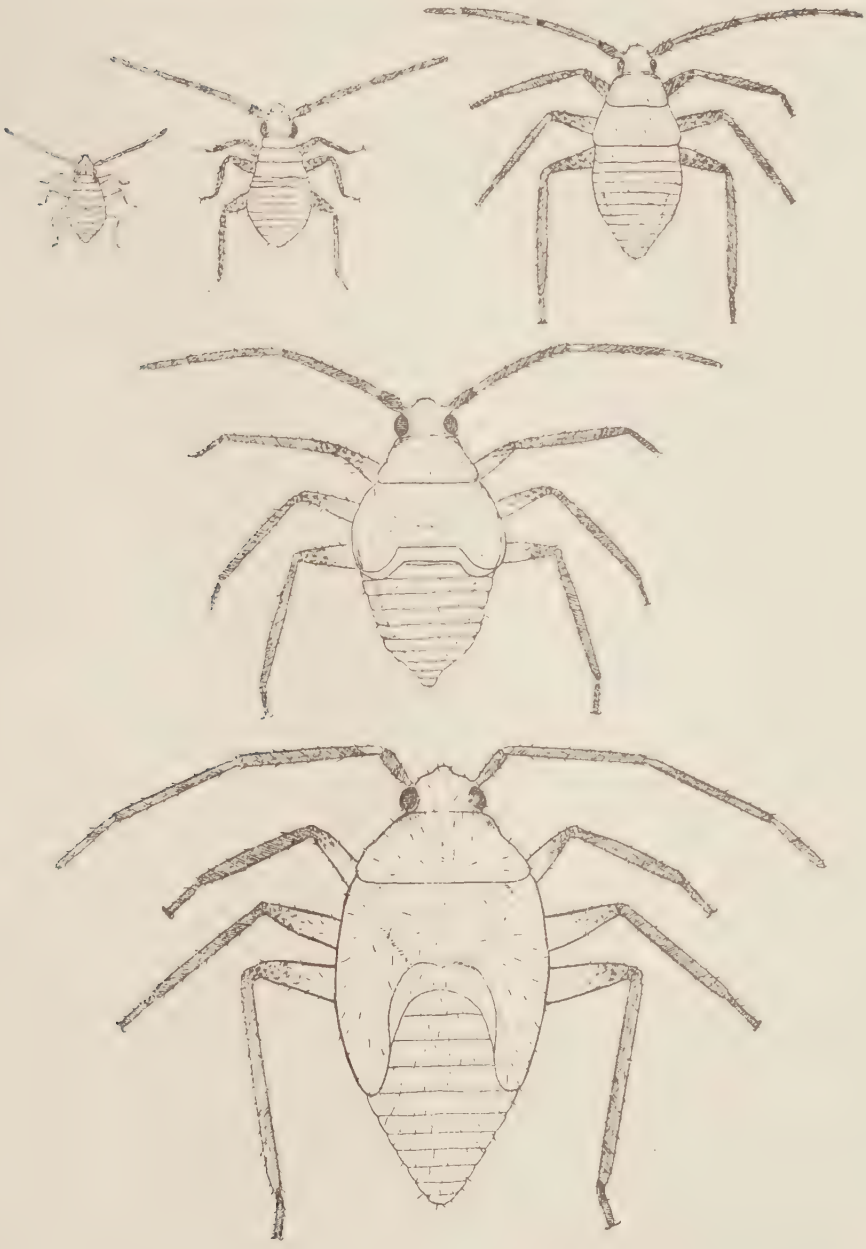


Fig. 2. *Lygus simonyi*, Reut. : 1st to 5th stage nymphs (x 12).

Shoot 1. 30 buds removed at random gave 28 healthy, 2 spotted. The shoot was then fed to bugs for 24 hours and the remaining buds separately removed and examined as before with the binoculars. Result—0 healthy, 60 spotted.

Shoot 2. 14 buds removed, all healthy. Shoot fed to bugs for 6 hours. Result—8 healthy, 46 spotted.

Shoot C2. 13 buds removed, all healthy. Shoot kept in cage without bugs for 6 hours. Result—16 healthy, 3 spotted.

Shoot 3. 21 buds removed gave 18 healthy, 3 spotted. One node was surrounded with cotton-wool to protect it from the feeding of the bugs, and the shoot was then introduced into a cage with bugs. After 18 hours the result at the unprotected nodes was 3 healthy, 58 spotted, and at the node protected with cotton-wool 11 healthy, 1 spotted.

In another case where a sleeve was placed on a shoot on the tree, without bugs, and left in position for some time the berries set and healthy buds numbered 62, and there were no black or spotted buds; while a shoot from the same tree, selected at random, subject to the feeding of the bugs present naturally, gave a count of berries set and healthy buds 28, buds black or spotted 12.

There is one final experiment in this series to record, which produced a singularly clear result. An attempt was made to demonstrate the damage by this bug at an Agricultural Show held in Nairobi in January 1931. A young coffee tree planted in a box was placed in a wood and muslin cage which had a glass door. A cloth sheet was then fixed so as to cut off the top right-hand quarter of the cage and 8 primaries of the tree were inserted through small sleeves in this cloth, which were tied round the primaries with string. The cloth was then nailed carefully all round and fixed with putty to the glass so that it should be insect proof. Capsids were then introduced into the cage, and the condition of the flower-buds subject to their attack and protected from it, both on the same tree, could be observed through the glass door. Although the tree did not flower at the time of the Show, it afterwards produced perfect flowers and set fruit on every one of the eight protected shoots, while on the rest of the tree the buds were early seen to turn black, and not one flower opened or fruit set.

Cause of Damage.

As soon as the bugs were first seen in any numbers on the trees, they were collected and provided with various parts of the coffee tree in the laboratory. They were seen to suck young flower buds with avidity, and while flower buds were present did not feed on any other part of the plant. If, however, flower buds were not available they fed on any fairly tender part of the plant, on young shoots or young berries. Later, however, as further observations on their feeding were made, it appeared that it is unusual for the bug to feed on anything except flower buds.

Dissections of buds which had been exposed in cages to *Lygus* feeding, made under a binocular microscope, early showed a minute spotting of the anthers. When the buds had been exposed for some days to the bugs the stamens were very heavily spotted and in cases had turned black along their whole length. Similar buds were later seen to turn completely black, owing to the early rotting of the stamens and subsequent blackening of the unopened petals. This forms a small black spike or cap to the bud, which is the typical form of damage as observed in the field. It sometimes happens that this black cap is removed a short distance away from the ovary, along the style which is white and undamaged; this is also an almost certainly diagnostic character of *Lygus* damage in the field.

The feeding was watched under binoculars on stamens placed in petri dishes. In the first two cases, with their controls, the styles and stamens were dissected from buds and seen to be white and completely unspotted, and were then introduced into

petri dishes. In the case of 3 and its control the buds were carefully opened down one side, the style and stamens examined and found to be unspotted and the buds were then closed up again as well as possible and placed in petri dishes.

			Result.
Dish 1 ...	Style and 2 stamens healthy.	3 adult bugs introduced into dish for 24 hours.	Style was not fed on and remained unspotted. Stamens spotted.
Dish C1 ...	do.	No bugs.	Style and stamens unspotted.
Dish 2 ...	3 stamens healthy.	6 nymphs introduced into dish for 24 hours.	All stamens spotted.
Dish 2C ...	do.	No bugs.	All stamens unspotted.
Dish 3 ...	4 buds healthy.	6 nymphs introduced into dish for 5 hours.	All stamens spotted. Style unspotted.
Dish C3 ...	do.	No bugs.	All stamens unspotted. Style unspotted.

In several cases the actual points where the bug fed on the stamens were noted, and at these points a spotting was seen to occur. It has been demonstrated by K. M. Smith[3] that the saliva of some Capsid bugs contains a principle which is violently toxic to plant life, and though it was not considered important in these investigations to make any detailed study of the effect of the bugs feeding on the stamens, the effect seems likely to be due in this case also to a toxic principle in the saliva. Some tentative attempts were made to induce spotting and abortion of the buds by inoculating them with salivary glands dissected from adult bugs. Either the time devoted to this work or the technique was inadequate, because no positive results were obtained.

Life-history Notes.

As the writer's work did not allow constant attention to be paid to this bug at any time of the year, a detailed biological study could not be made. The following notes alone, therefore, are available.

The only food-plant at present known is coffee. It seemed probable that some indigenous plant would prove to be the original host, but search has not yet revealed one. The egg is inserted into the coffee bud, and is completely hidden, the cap not protruding and only a small scar marking the place. The eggs are thus impossible to detect in the field and can only be found by dissecting buds under a binocular microscope. The bug breeds with difficulty in the laboratory; in several cases eggs were laid but in no case did these hatch. Also first instar nymphs usually died in captivity. From the second instar to the adult, however, the bug lived on coffee in the laboratory. The times of the different instars varied very considerably, probably owing to the different condition of the coffee available as food in the laboratory, since coffee with flower spike could not always be provided. Thus instars 3 and 4 varied between 3 and 7 days, and instar 5 was fairly constant between 10 and

14 days. The adult lived for three weeks caged on coffee, but its life in the open may be longer.

In the plantation the bugs may be found in all stages at any time, the temperature being suitable for their reproduction throughout the year. The nymphs are usually found in the buds and blossom spikes and when disturbed run rapidly along the branches from node to node. The early instars are very small and are not easy to see on the tree. The nymphs do not drop to the ground readily, and considerable shaking and jarring is required to make all of them fall. The adults are also usually to be found in the blossom clusters, but they fly readily when disturbed; and they are often seen in flight in the mornings and evenings. During the heat of the day they usually take up a shady position inside the tree.

The natural enemies of *Lygus simonyi* at present known are few. A small Lygaeid bug, *Geocoris ruficeps*, Germ., is known to prey on it, but this bug has only been seen singly and occasionally.

Two or three species of spiders have been seen to capture individuals of the Capsid, but though there are often large numbers of spiders of many species on the trees, this prey seems quite accidental.

In three cases the larva of an internal parasite was dissected from a nymph. In no case has the adult been bred, and the identity of the larva could not be ascertained in any of the three cases observed. This parasite is distinctly a rarity at present.

It may be said that none of these enemies sensibly affected the numbers of the bug during the year.

Factors influencing the Numbers of Bugs and the Damage caused.

As the temperature throughout the year is suitable for the breeding of the bugs, the chief factor governing their increase is the presence of coffee spike. Thus throughout the year bugs in all stages were found, but the number present during and directly after the March-April blossoming was much greater than at other times, and there was a similar increase at the time of the September-October blossoming. Rain seemed not to have any direct influence on the bug, but its influence may be indirect by inducing flowering of the coffee. Thus in two of three cases where *Lygus* was present in exceptionally large numbers it was during the " long rains " at the time of the April blossoming, and in the third case in another district it was in September when flower spike was present, although it was during a prolonged dry period.

The damage that the bug is capable of doing depends largely on the type of blossoming of the coffee, and the peculiar climatic conditions of 1930 in the Kiambu district seemed to predispose the coffee to an attack of great severity. In this district it is normal for the main flowering to occur some time near the beginning of the long rains in March or April, and this should be a very heavy and general flowering, representing the bulk of the crop for the year. From this time till the beginning of the " short rains " in September there is normally no flowering, but in September or October another flowering, fairly heavy, but less than the March-April one, takes place. After this again there is no real flowering till March. Normally then almost the entire crop is the result of these two flowerings. In such a case the bug, if present, would take a toll of the flowerings, but would be unable to increase sufficiently quickly in numbers to do serious damage before the majority of the blossom had set satisfactorily.

In 1930, however, there was not one general flowering in March or April, but the coffee made repeated " spikings " during several months. And at the end of September there was on most estates a fair blossoming, followed again by many abortive blossomings.

Owing to the kindness of a well-known planter who observed his coffee very carefully, I am able to give the following facts of the blossoming and " set " on his estate for the year :—

" March. Earliest flowering in 1930. Fairly good, about 60 per cent. of the normal set.

" From this time on the trees continually tried to flower and nearly all this turned black and failed to set.

" Thus—

" April. Little set.

" May, June. Constant attempts to flower about every 15 days. None set.

" July, August. Dry months—no flowering.

" September. At end of September and beginning of October a blossoming. Fair, about 50 per cent. of the normal set.

" Another blossoming in middle of October. Poor, perhaps 20 per cent. set.

" November, December. Coffee tried to flower. None set."

During the whole period from after the first March blossoming until June, *Lygus simonyi* was present here in large numbers and was maintained by the constant flowerings and able to destroy the majority of them. In July, August and September, when there was no flowering, their numbers fell very markedly, although they were still present during this period. Owing to the decreased numbers of the bugs the first September-October flowering set to the extent of 50 per cent., but owing to another marked increase of *Lygus* at the time of this blossoming most of the later blossomings were destroyed. The constant " spikings " may have been stimulated partly by the fact that no fruit was set owing to their constant abortion, but observations where Capsids were scarce showed that the normal condition of two blossomings was upset by some other factor, probably climatic. For the " epidemic " flower failure both the bug and abnormal flowering conditions seem to be necessary. The bug is the agent, while the conditions are the cause.

Other Causes of Failure of Blossoming.

Where the Capsid is not present, a small percentage of flower buds does not set, for unknown reasons, and this is, of course, a recognised condition with many plant species. In the case of coffee there are many atypical blossom buds, some of which are able to set fruit satisfactorily, and some which probably do not set.

When the bud at a node is in the stage of a single swelling containing undeveloped all the flowers from that side of the node, it is not unusual for it to be covered thickly at the end by a waxy secretion, which on dissection is seen to be present also inside the bud. It is generally considered that this condition is abnormal and results in a failure of the flowers from the bud. Further research on this peculiar condition is necessary. Here it may be said that the condition has never been produced experimentally by the bug, and that certain of these buds which were marked did produce normal flowers, which set fruit.

When the bug was first evident, in numbers, there was a considerable amount of " star-blossom " on many trees. In this condition the flower seems to open before the petals have reached their full development, producing a peculiar little star-shaped flower. This condition also is not connected with bug injury and a large percentage of " star-flowers " which were marked finally opened normally and set fruit.

The only abnormal condition in the flower-bud not caused by the bug, which is definitely known to result in its abortion, was discovered during the examination of buds for *Lygus* damage. This is a rotting of the style, which takes place at a very early stage of the bud's development, when it is a minute green spike. In such cases the style is rotted with a uniformly coloured brown rot, usually near its base. The cause of this is not known, but it has never been produced in shoots exposed to the feeding of the bug ; it is not in the form of spots which are diagnostic of early Capsid

injury, and it often occurs in buds the stamens of which show no spotting. The percentage of buds thus affected is usually very low, in most cases being less than 1 per cent.

In general it may be stated that *Lygus simonyi* was the cause of the great majority of the loss of crop due to flower abortion in 1930.

The seriousness of this pest may be judged by the following estimate of the actual loss of crop for the year, on certain estates, due to this flower-bud abortion :—

Estate 1	50	per cent.	decrease.
2	25	,,	,,
3	50	,,	,,
4	50	,,	,,
5	50	,,	,,
6	95	,,	,,
7	40	,,	,,
8	60	,,	,,

For the estimate in the first five cases I am indebted to Mr. R. E. Lane, a professional adviser in coffee-growing. In the case of Estate 6, the trees were in splendid condition to bear a heavy crop, and there was great promise from the amount of young spike. *Lygus* was present, however, in particularly large numbers, and an almost complete loss of crop occurred. In the case of Estate 8, which was studied very closely, the average number of bugs at and after the March blossoming was about 200 to a tree ; the numbers fell during the dry weather to about 30 to a tree, and increased again on the October flowering until at the beginning of November there were 100 to a tree.

Distribution of Lygus simonyi.

The writer has been kindly informed by the Director, Imperial Institute of Entomology, that *Lygus simonyi* has been recorded from the following localities : Aden, Kilimanjaro, Kibonoto, Moshi, Meru Plains, Madagascar, Caffraria, Cape Town.

In Kenya the first record of this bug, so far as is known, is the writer's from Kiambu, in March 1930. The bug had, however, been known to be present on coffee in small numbers from June 1929, but was not collected or identified at that time. It may have been, and most probably has been, present on coffee as a minor pest for some years, since some planters recognise the widespread abortion of flowers in 1930 to be similar to a less serious condition noticed previously. The following extract from a letter from a planter to the Entomologist, dated 27.vi.1927, is of interest :—

> " While smoking for *Antestia* I noticed quite a number of small, bright green insects, about one-tenth of an inch long, quick runners, but apparently do not hop or fly. Can you give me any information, please ? "

The identity of these insects cannot be ascertained, but the description applies well to the nymphal stages of *Lygus simonyi*, and it does not seem unlikely that it referred to this insect.

The bug seems to be widely spread throughout the country, and early in 1930 it was present in large numbers in several districts, in all of which serious damage occurred. This is additional evidence for believing it to have been widely spread previously. The writer has found the bug in the following districts :—Kiambu, Ruiru, Thika, Makuyu, Limuru, and Nyeri, and specimens have been received from Fort Ternan and Koru. A large number of other records were received, but some of these may have referred to another species.

The bug has been seen on coffee at altitudes from 4,500 ft. to 6,500 ft., and though generally it was more serious at the higher altitudes, one very heavy attack was at about 5,000 ft.

Other Capsid Pests of Coffee in East Africa.

The only other Capsid known previously to damage coffee in East Africa is *Lycidocoris mimeticus*, R. & P. This bug feeds on the growing points and young foliage of coffee in Uganda and Tanganyika and sometimes causes serious damage.

Hancock[4] reports :—" The growth of the trees was so badly distorted that no crop could be produced, and it was recommended that all the affected trees be stumped immediately."

And Ritchie[5] :—" The Capsid bug, *Lycidocoris mimeticus*, R. & P., causes considerable damage called ' bug wither tip ' to young growth of *C. arabica* . . . by puncturing the growing tips and young foliage, causing death."

Reference has already been made to the five species of Capsids that feed on coffee flower-buds in Uganda, which are not considered to cause flower-abortion.

It would be expected that coffee in Tanganyika would suffer from injury by *Lygus*, because it has been recorded from several of the coffee-growing districts of that country. There is no record of this, however, and the writer made a careful search for it in coffee on the southern slopes of Kilimanjaro in February 1931, without success. One solitary nymph was found, which merely confirmed the fact that the district is within its range. There was, however, hardly any flowering present at the time of the visit.

Two other species of Capsids, at present unidentified, were found to feed on coffee during the course of the observations on *Lygus simonyi*. One species (T 303) was present in small numbers, up to 4 to a tree, on one estate in November 1930. It was apparently not very generally distributed. Like *Lygus simonyi*, it feeds chiefly on blossoms and may do similar damage but has not yet been present in sufficient numbers to be noticeably harmful.

The other species (T 325) is present on many estates, but only an occasional bug is seen. In the laboratory it feeds chiefly on tender shoots and leaves, but no damage has been proved against it.

Control Measures tested.

Although the preliminary experiments with a control measure which promises considerable success are to be described in some detail, it is of interest to describe those other methods which proved either unsuccessful or impracticable.

Contact spraying immediately suggests itself for the control of this bug. But in the case of coffee in Kenya, a closely planted crop with between 500 to 700 trees to the acre, plantations usually of more than 100 acres and sometimes nearly ten times that area, with difficulties of water provision and transport, and of unskilled native labour, the attempt must first be made to control any widespread pest by other means than contact spraying. And *Lygus simonyi* offers more difficulties than most other coffee insects to control by other means.

It is not possible to " hand-pick " the insects, because in the early nymphal instars they are so small as to be almost invisible in the coffee buds. A native trained in catching insects obtained not more than 200 to 300 a day for the experiments described herein, on an estate where detailed counts showed the average number to a tree to be over 100. It is the habit of various other bugs to run along the primaries and down the trunk of the tree when smoke is applied below, and collecting is thereby facilitated. Such smoking disturbs *Lygus* but little, and it does not come down the tree.

An investigation was made of the possibility of removing the bugs by jarring the tree and killing those that fell. A similar method is suggested by Petherbridge & Thorpe[6] for use on a small scale against *Lygus pabulinus*. It was found impossible by shaking and jarring the tree to bring down a large number of bugs. When it was first tried, two boys took 5 minutes to a tree to shake off and kill over 100 bugs. But by this method it is not possible to clear the tree completely without the expenditure of much time, and causing some damage to the tree. The method was tried on a fairly large scale for three days, and an average of about 10 or 12 bugs to a tree was left. This costs about 10*s*. an acre for labour, and owing to the number of bugs left is probably not a useful measure.

An experiment was made with the poison bait used against the Pentatomid *Antestia*. When caged in the laboratory, if starved, *Lygus* would suck up a dilute sugar syrup, but the application of the *Antestia* bait (sodium arsenite 1 oz., jaggery 2½ lb., water 4 gallons), both painted on the trunks and sprayed on the foliage, was inefficacious. The greatest number of bugs found dead after its application was 12 from one tree, at a time when the average number to a tree was about 100. It appeared that *Lygus* will not suck sugar, except accidentally, if flower-spike is available.

Some experiments with contact washes and with dusts were made. A miscible-oil spray, prepared by the Agricultural Chemist, containing the toxic principles of pyrethrum, was used with success. It is found that for average-sized trees of full-bearing age about 2 gallons of wash are necessary to ensure that the tree is sprayed sufficiently thoroughly to kill all, or nearly all, the bugs present. This makes contact spraying of coffee expensive and troublesome.

Dusting with powdered pyrethrum, and with a proprietary nicotine dust, also gave some moderately successful results. Both the dusts were toxic on contact, and this method seems chiefly limited by two disadvantages, firstly the difficulty of having the dust applied sufficiently thoroughly to kill all the bugs present, and secondly by the cost of the measure, which, though not accurately ascertained, would seem to be high.

A small experimental application of "Cyanogas" dust, without enclosing the tree in any way, showed that by this means *Lygus*, *Antestia*, ants and many other insects on the coffee tree can be readily brought down. There is a large percentage of recoveries, however, and its application would seem to offer considerable danger to native labour.

Extract of Pyrethrum in Paraffin.

A method which lacks many of the disadvantages pointed out in the measures described above, and promises to be an effective and comparatively inexpensive control, is spraying with an extract of pyrethrum in paraffin, undiluted.

The spray is prepared by adding 1 lb. of pyrethrum powder to 1 gallon of paraffin, shaking or stirring vigorously at intervals for at least 24 hours, then filtering, to make a clear solution for spraying. By this means much of the toxic principles in the pyrethrum powder is extracted, and the liquid has been shown to be a potent insecticide. This simple method of preparing the spray has been shown to be quite effective, and it is an advantage for the planter, with no technical knowledge or complicated machinery, to be able to prepare it himself with a minimum of trouble and expense. It is applied to the trees at a low pressure by using a small hand-sprayer, in which a horizontal piston gives a blast of air which draws the liquid up a vertical tube and delivers it in a fine mist. There are several small inexpensive and efficacious commercial hand-sprayers of this design. A number of pumpings around and inside the coffee tree produces a sufficiently penetrating mist to ensure that the majority

of the Capsids on the tree are hit with a small quantity of the spray. Usually within three minutes the Capsids fall from the tree, and though a large number live for several hours on the ground, the percentage that recovers is minute.

One of the most advantageous features of this spray is the extremely small quantity required for an acre of coffee. To spray an acre of 680 trees of full-bearing age requires between 2 and 3 gallons of the spray according to the size of the trees. The difficulties and expense of water transport inherent in the use of contact washes in water-solution are saved. Two "water-washes," one a proprietary preparation, and the other an infusion of local native tobacco were tried at the same time as the pyrethrum-paraffin mixture. It was found that though both were toxic to the Capsid, it was necessary to secure thorough wetting of the whole tree in order to kill all the insects, this would entail almost as large a volume of wash for each tree as is required of pyrethrum-paraffin spray for an acre.

The present rate of work is about one-third of an acre by one boy in a day, which makes the labour costs about two shillings an acre. There is as yet no quotation of the cost of the materials bought in large quantities in this country, but the cost of the spray should not exceed five shillings a gallon. The cost per acre is considered trifling in comparison with the loss caused by a large number of the bugs.

A number of proprietary sprays usually employed for killing mosquitos in houses, most of which appear to be extracts of pyrethrum in an oil, and analogous to the pyrethrum-paraffin spray described, have been tried, all with some success.

The following table gives the results of a comparison of the pyrethrum-paraffin spray and a proprietary spray numbered 1. The spraying was in two different blocks of coffee; at the time when this trial could be made there were comparatively few bugs on the trees.

	Pyrethrum-paraffin		Proprietary 1	
	Number of trees sprayed	Average number of bugs killed per tree	Number of trees sprayed	Average number of bugs killed per tree
Block 1	9	25	9	16
,, 2	5	42	6	40
Total ...	14	31	15	26

In block 2 the same trees were again sprayed two days later, and thoroughly shaken to remove all bugs, the average number of bugs obtained was 1·8 in the case of the pyrethrum-paraffin, and 2·0 in the case of the proprietary spray.

A small trial of the pyrethrum-paraffin spray with several other proprietary sprays, and also pure paraffin was made. The results were :—

Spray	Average number of bugs killed per tree; three trees sprayed in each case
Pyrethrum-paraffin	30
Proprietary 2... ...	22
,, 3... ...	27
,, 4... ...	28
,, 5... ...	27
,, 6... ...	25
Paraffin	2

From the above figures it appears that the pyrethrum-paraffin spray and all the proprietary sprays are not greatly different in efficacy. Though the figures for the pyrethrum-paraffin spray are slightly higher than for the others, a significant superiority cannot be demonstrated from these figures. But even if it is only equal in efficacy to the proprietary preparations, it has the advantage of a very much lower cost. Experiments using different proportions of pyrethrum are planned, but as the spray is not costly to prepare, it is unlikely that it will be found advantageous to reduce the proportion of pyrethrum powder appreciably.

An opportunity occurred of making observations when a commercial application of Proprietary spray 1 was being made, at a time when the bugs were present in large numbers.

Several blocks had been sprayed, using different quantities of the spray. The trees were very large and required a full three gallons an acre. The average number of bugs to a tree was about 200. In a block that had been sprayed with 2 gallons of spray an acre, tests on a few trees later showed an average of 30 bugs to a tree, and where 2½ gallons an acre had been applied, the average two days later was 7.

Three trees were then selected at random and a fourth because of its large amount of flower-spike, and these were sprayed at the rate of 3 gallons an acre, the figures were :—

Tree	1	114	bugs killed.
,,	2	101	,, ,,
,,	3	60	,, ,,
,,	4	301	,, ,,

And the average number of bugs left was 2 to a tree. These figures show clearly that it is important to apply an amount of spray adequate for the trees, and this chiefly depends on their size. If the amount applied be adequate it seems to leave only a few bugs, and about the same number 2 or 3 to a tree, whether the number present on the tree at the start was large or small.

Detailed recommendations as to the best times to spray cannot yet be made. The spray has still to be tried before an important flowering.

A large number of other insects are killed by the spray, including *Antestia*, leaf-eating beetles, some COCCINELLIDAE, and many others. The percentage of *Antestia* killed did not appear to be high enough to warrant the application of the spray against this insect alone. Its use also would probably not reduce the number of beneficial COCCINELLIDAE very significantly. On the whole it appears at present that, other than *Lygus*, more harmful insects are killed than beneficial. Cases where a beneficial predacious or parasitic insect was present on the trees in numbers might occur, which would have to be specially considered.

The danger of scorching the tree with such a spray must be studied. The amount of scorching varies with the brand of paraffin, and seems to depend chiefly on the aromatic content. Thus a good lighting paraffin, from which the greater part of the aromatic constituents have been removed, in order to reduce its tendency to smoke, was found to scorch very little, while another paraffin with a higher aromatic content scorched more seriously. Such a paraffin therefore, from which the greater part of the aromatic constituents have been removed is to be recommended for this purpose, even though no serious scorching occurred with any brand used, when the spray was applied correctly, as a fine mist. At most an occasional leaf or tip, which happened to receive a direct spraying, has been scorched, but this damage is negligible. Damage to buds likewise only occurs when a drenching spray is applied. It may be mentioned that several of the proprietary sprays burn the tree very seriously, and none burns less than the pyrethrum-paraffin mixture. As it is not possible to state definitely that no serious scorching can occur in any conditions, each planter is advised to satisfy himself that serious scorching does not occur in his conditions.

It is suggested that this use of pyrethrum and possibly other insecticides in a petroleum oil solvent, entailing as it does the use of such a small quantity of spray, may be of much wider application. There would seem to be a number of bugs that, like *Lygus*, could be economically killed on a field scale with such a spray, particularly in cases where they are at present controlled by expensive contact washes.

Summary.

1. A serious form of coffee flower abortion that occurred in Kenya Colony in 1930 is described.

2. A Capsid, *Lygus simonyi*, Reut., is shown by experiments to be capable of causing this abortion.

3. It is shown that by feeding on the stamens at an early stage in the bud's development, the bug causes their early blackening and abortion, resulting in the complete failure of the flower.

4. Some notes on the life-history, habits, and natural enemies are included.

5. It is shown that owing to abnormal flowering conditions in 1930 the bug was enabled to do very serious damage.

6. Some other abnormal conditions of the buds, not considered to be caused by the bug are described.

7. A number of control measures that proved unsatisfactory are shortly described.

8. A detailed description is given of the application of a spray prepared by extracting the insecticidal properties of pyrethrum with paraffin. This spray is inexpensive, easy to apply quickly, and seems likely to prove efficacious on a large scale.

9. It is suggested that such sprays may have a considerably wider application.

My acknowledgements are due to the Senior Entomologist, Mr. T. J. Anderson, for kindly reading the manuscript; also to a large number of coffee-planters, in particular to Mr. P. J. Coldham, on whose estate much of the above work was done, and to whose interest and help, particularly with regard to cultural questions, I owe much.

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Fig. 1. A healthy coffee branch.



Fig. 2. A branch attacked by *Lygus simonyi*.

The effect of Lygus simonyi on coffee.

AN ECOLOGICAL STUDY OF THE "LUCERNE FLEA" (*SMYNTHURUS VIRIDIS*, LINN.)—I.

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Contents.

		Page
I.	Introduction	102
	1. Geographical distribution	102
	2. Nature of the damage	103
	3. Food-plants	103
	4. Economic significance	104
II.	Life-history and bionomics	104
	1. Seasonal history	104
	2. Method of rearing	106
	3. Number of instars	107
	4. Duration of stadia	108
	5. Length of life-cycle	108
	6. Growth of nymphs	109
	7. Oviposition	112
	8. Hatching	113
	9. Sex ratio	113
	10. Significance of life-history studies	114
III.	The method of investigating environmental factors	114
IV.	Effect of biotic environmental factors upon survival	116
	1. Insect predators	118
	2. Spider predators	122
	3. Comparison of Insect with Arachnid predators	124
	4. Effect of density upon rate of population increase	126
V.	Effect of physical environmental factors	127
	1. Effect of temperature upon growth rate and total growth	127
	2. Effect of humidity upon growth rate and total growth	130
	3. Effect of soil pH value upon growth rate and total growth	132
	4. Effect of various combinations of temperature and humidity on fecundity	135
	5. Effect of soil pH value upon fecundity	138
	6. Effect of soil type upon choice of site for oviposition	139
	7. Effect of temperature upon longevity	140
	8. Effect of humidity upon longevity	142
	9. Effect of soil pH value on longevity	143
VI.	Inter-relationship of different phases in the life-cycle	143
VII.	General survey of environmental effects upon *Smynthurus*	144

I. Introduction.

The agricultural importance of the Collembola has in the past usually been regarded with some scepticism by economic entomologists. Recently, however, the activities of certain species, particularly those belonging to the genera *Bourletiella* and *Smynthurus*, have resulted in an increasing amount of publicity for this order of primitive insects. The subject of the present investigation is *Smynthurus viridis*, Linn., which, from its jumping habits and the depredations it causes to lucerne (alfalfa), has come to be known commonly as the "Lucerne Flea," although the damage it causes to clovers is equally serious.

On the establishment, in 1927, of Farnham House Laboratory by the Imperial Institute of Entomology, for which funds were supplied by the Empire Marketing Board, for the biological control of insect and plant pests, one of the first demands for parasites was that from Australia for the Lucerne Flea. Accordingly, Dr. J. G. Myers commenced investigations with a view to obtaining an effective biological factor of control, and while several predatory species were obtained, the dissection of numerous specimens, in the hope of discovering parasites, was without avail. It was evident, however, that a thorough investigation into the natural controlling factors of this species was an essential preliminary to assessing the significance of those predators as natural agents of control, and their consequent utilisation on a rational economic basis. This task was assigned to me by Dr. W. R. Thompson on my arrival at the Laboratory, working under a Research Scholarship from the Ministry of Agriculture and Department of Agriculture for Scotland, at whose request I was granted accommodation.

Previous to the commencement of this investigation *Smynthurus viridis* had been described, and various anatomical structures figured, in the works of several authorities on the taxonomy of Collembola, but all that was known concerning the biology of the species was contained in two papers, one by Davies[4], working at Rothamsted in this country, and another by Holdaway[10], working at Adelaide University in South Australia, and though both these workers concentrated on the life-history of the insect, practically no information of a quantitative ecological character was available. Hence this paper, while embodying considerable additions to a knowledge of the life-history and bionomics *in sensu stricto*, is largely devoted to a determination of the rôle of environmental factors in limiting the normal increase of the *Smynthurus* population in nature, and the data obtained therefrom have been utilised in the construction of a theoretical distribution map for the species. In concluding, an attempt has been made to elaborate some general principles on the intricate and difficult problem of natural control, the writer agreeing with Woodger[21] that "we are in danger of being overwhelmed by our data and of being unable to deal with the simpler problems first, and understanding their connection. The continual heaping up of data is worse than useless, if interpretation does not keep pace with it."

1. Geographical Distribution.

Smynthurus viridis has a wide, but also a rather peculiar, distribution, being restricted to two bands of territory running approximately parallel to the equator, one in the Southern, and the other in the Northern Hemisphere. In his monograph on the Collembola, Lubbock[14] states that it occurs in Sweden, Switzerland, France, England, and Germany. The known distribution has considerably increased since then, and it seems almost certain that the insect has been introduced from Europe to those countries in which it is now found in the Southern Hemisphere. By referring to a variety of literature I have been able to augment Lubbock's known distribution of the species (by countries) as follows:—Russia (Arctic Ural), Rumania, Spitzbergen, Italy, Finland, Hungary, Algeria, Morocco, Iraq, Denmark, and almost the

whole of the British Isles, while in the Southern Hemisphere, it occurs in Argentina, Australia and Tasmania. The distribution in Australia is at present restricted to South Australia and the south-west of Western Australia, and it is only within the last few years that it has been recorded from Tasmania. There seems no reason why the species should not extend to certain other parts of Australia, as well as a few other countries in the Southern Hemisphere, unless definite measures are taken to prevent its spread, but this subject will be treated in greater detail in a subsequent section.

2. Nature of the Damage.

The depredations of this springtail have undoubtedly been overlooked, owing in part to the attribution of the damage to other species, such as *Apion*, *Sitona*, and probably slugs, and because the elusive habits, small size, and coloration, tend to make this species very inconspicuous to the eye of an untrained observer. Even when one has gained some familiarity with the insect and then attempts to observe specimens in their natural environment, the population may appear to be very sparse compared with its true density. The actual damage consists of a skeletonisation of the leaf surface in severe cases, brought about through the chiselling and rasping action of the insect's mandibles and maxillae in the course of feeding, while partly eaten leaves are soiled by the excrement and rendered distasteful to stock where the springtail is present in very large numbers, as in Western Australia. Sometimes the attack commences from the upper surface of the leaf, sometimes from the lower surface, or indiscriminately from either, depending on the plant attacked and the protective armament on its leaf surface, such as hairs, wax, etc. In either case the epidermis is stripped off, the underlying mesophyll eaten, and the adjacent epidermis left as a mere skeleton, which serves as a support for the insect in the furtherance of its depredations.

3. Food-plants.

Smynthurus has a tremendous variety of food-plants, including such diverse families as Urticaceae, Cruciferae, Polygonaceae, Compositae, Graminaceae, and Leguminosae. Indeed the only factor which inhibits its attacks is morphological structure, the physiological characteristics of most plants being quite incapable of affording protection, although they affect to some extent the growth rate and general well-being of the insect, which seems to thrive best on species belonging to Leguminosae, together with a few members of the Compositae. Cape Weed (*Cryptostemma calendulaceum*) seems to be a favourite food-plant in Australia, and the writer has observed *Centaurea nigra* and *Achillea millefolium* as favoured Compositae in this country; but the Leguminosae have pride of place in this connection, and *Smynthurus* has been observed flourishing on so many members that it would appear capable of thriving on any species in this family. Plants having a broad leaf expanse with few veins make good subjects for *Smynthurus* attack, whereas narrow-leaved species, with close set veins, such as are found among grasses, are much less liable to injury, although by no means immune. In the latter instance the insect has to chisel in a longitudinal direction between the vascular strands, being held up by the tougher nature of the bundles if it attempts to cross them.

During the summer of 1929 a trial was conducted with the object of obtaining a variety of lucerne which was less susceptible to injury than the others, since it was thought that perhaps a very hairy-leaved variety might resist attack to some extent. However, out of the nine varieties tested, only one, namely "Hairy Peruvian" (from Arizona), seemed to exhibit fewer signs of injury than the others, and the difference was not sufficient to warrant the replacement of another variety, which, from its general characteristics, the agriculturist finds highly suitable to his particular conditions.

From field observations and experiments conducted in the laboratory *Smynthurus* is undoubtedly selective in its feeding habits, preferring legumes if these are available, and thriving best, in this country at least, on members of the genus *Trifolium*, especially *repens*, including all its varieties. It should be mentioned here that although *Smynthurus viridis* and one or two others are exceptions, the phytophagous habit of feeding is not characteristic of the order Collembola, the vast majority of species being saprophytic and a few carnivorous, such as *Anurida maritima*, *Isotoma sepulchralis*, and *I. macnamarai*.

4. Economic Significance.

The first authentic record of *S. viridis* being of economic significance is that of Froggatt,[8] who mentions that in 1896 a species allied to the European *S. viridis* appeared in countless millions in lucerne paddocks in South Australia. Although there has been some doubt as to the identification of the insect in South Australia, it seems to be fairly well settled now that the species there is none other than the common European *S. viridis*, exhibiting a variation in the different environment; for it varies very considerably with the season even in the South of England.

After several experiments designed to determine the cause of their seasonal colour variation, the writer found that it was not due to light or humidity, but seemed to be a temperature effect, brought about through its influence either on the distribution or composition of the green pigment, to which the insect owes its colour. As the nymph on hatching is pale yellow and remains so if green food is withheld, there seems no doubt that the green colour of the insect is due to chlorophyll or a derivative.

In 1920, Lea[13] reported that "the lucerne flea is troublesome in some years in S. Australia," and subsequent reports from the same author, and Newman in Western Australia, have served to emphasize the serious nature of the damage caused by this pest in Australia. In England, a few outbreaks have been recorded in the "Monthly Reports of the Ministry of Agriculture," but to the average agriculturist *Smynthurus* is unknown. From observations conducted in several counties in Scotland the writer was able to ascertain that *Smynthurus* is of greater economic importance there than in England, some pastures being so heavily infested that one could not find a single clover leaf which did not exhibit traces of *Smynthurus* damage.

II. Life-history and Bionomics.

Very little is known concerning the biology of the Collembola as a whole. *S. viridis* seems to have received more attention in this respect than any other species, and the life-history has been worked out in Australia by Holdaway, who has also described the egg, nymph, and adult stages in considerable detail, so that it will be unnecessary to repeat those descriptions here. However, no one has described the course of events occurring under the very different climatic conditions of this country, to which *Smynthurus* is peculiarly susceptible, so this will be presented in some detail.

1. Seasonal History.

Observations were commenced at the end of September 1928, and continued till July 1930, although most of the data presented were derived from the first year's work, the field observations of the second year being largely utilised as a check on those of the first year, and to confirm conclusions derived therefrom. Three separate fields in the neighbourhood of the Laboratory were utilised for the purpose of making general observations on *Smynthurus* and deriving quantitative estimates of the

population, together with sweepings of lucerne and soil samples obtained by Mr. de Rippas, a field assistant on the staff of Farnham House Laboratory working in the South of France.

A gradual decrease in the *Smynthurus* population took place from 10th October (the time at which a census was first made) till 21st December, after which not a single specimen could be found in the fields until 10th April, when nymphs were obtained for the first time since the previous September. From 10th April there was a gradual rise in numbers till 26th June, and subsequent to this the level of the population underwent a series of violent fluctuations, correlated with the rainfall.

Since *Smynthurus* could not be found in the fields for three months of the year, namely January, February, and March, it seemed evident that it must pass the winter in the egg stage. This was proved conclusively as follows: A piece of clover turf was cut from the outdoor insectary, where the insects had been numerous in the previous autumn, and brought into the laboratory, where a thorough examination for *Smynthurus* was made in order to make certain that there were no adult survivors. Not a single specimen could be seen. The turf was then placed under a bell-jar and left in a room where the temperature varied between 7° and 15° C. (approx.), and in three weeks' time numerous nymphs were observed crawling up the side of the glass jar. The gradual reduction of the *Smynthurus* population with the advance of winter is thus due to the non-replacement of a generation which is gradually dying out by a subsequent generation, on account of the inhibiting influence of low temperatures upon the development of the egg stage. This affords an interesting illustration of how an insect may survive unfavourable periods under vastly different climatic conditions. Here, the unfavourable period is the winter, when development is inhibited on account of low temperature, while in South and Western Australia the unfavourable period is the summer, when development is inhibited on account of low relative humidity. In both cases the insect survives in the egg, which, when undeveloped, is extraordinarily resistant to high temperatures accompanied by low relative humidities, as shown by Holdaway in Australia, and is equally resistant to low temperatures, which was demonstrated by the writer as follows :—

A batch of 60 eggs, laid by one female, were allowed to develop in a saturated atmosphere, at a temperature ranging between 17° and 22° C., for 7 days. On the seventh day, development had proceeded to an extent which enabled one to see distinctly the eyes of the embryonic nymphs shining through the chorion. The eggs were then placed in cold storage at a temperature varying between 0° and 4° C., on 5th December 1928, and allowed to remain there until 15th February 1929, when they were brought into the laboratory. The temperature to which they were now subjected varied between 10° and 15° C. (obtained from a continuous chart record), and they were left there till hatching took place. Nymphs began to emerge on the morning of 2nd March, and continued to emerge until the end of the next day; 100 per cent. emergence occurred. The experiment demonstrates conclusively that partly developed eggs are quite unharmed by low or, what is of more importance in this country, fluctuating temperatures (at least those whose amplitude falls within the range 0°—20° C.), since the eggs were taken directly from 20° C. to 0° C., and from 0° to 15° C., without any gradations. All that occurs, evidently, is the temporary arrest of development, which again proceeds normally whenever the temperature rises above the developmental zero. The practical significance of the experiment is that it demonstrates :—

(1) The extraordinary vitality of the eggs—resistance of undeveloped eggs to dry conditions, as shown by Holdaway, and of partly developed eggs to freezing and fluctuating temperatures between 0° to 20° C., as shown above.

(2) That eggs would be quite unharmed during winter or spring despite the alternation of cold and fairly warm spells such as is commonly experienced in this country.

Seldom do we come across examples in the animal kingdom of an egg which is equally capable of immediate development or of resisting both freezing and desiccation, according as the conditions presented are favourable or otherwise, such exigencies usually resulting in elimination or being met by the production of eggs of a different type, when the life-cycle is carried over the unfavourable period in the egg-stage, *e.g.*, the "immediate" and "resting" eggs of Rotifers; also the "winter" and "summer" eggs of freshwater Cladocerans and Copepods.

Following the emergence of the first generation in spring, sometime in the middle of April, varying in either direction with environmental conditions, there are five subsequent generations. The second generation appears about the end of the first week in June, the third generation about the beginning of the second week in July, the fourth about the end of the second week in August, the fifth about the beginning of the second week in September, and the sixth about the middle of October. A point of interest with regard to the seasonal cycle of events is the gradual shortening of the time required for the appearance of the successive generations throughout the summer and early autumn, due to the rapid speeding up of metabolism by increasing temperature as the season advances. It should also be mentioned that there is very great diversity in the maximum size attained by the generations, this being largely dependent on rainfall, as will be shown in a subsequent section. The cycle of events in nature as outlined above have been described from observations conducted during a somewhat abnormal year, namely 1928–29, so that during years characterised by wet summers, or mild winters, one would expect that while the general course of events would be the same there would be considerable differences in the time of appearance and size of the respective generations, and this has been confirmed by observations carried on in 1929–30. For example, in 50 strokes with a sweeping net in Field A on 26th November 1928, 29 *Smynthurus* were taken, whereas in the same field subjected to the same treatment, 115 *Smynthurus* were obtained in 50 strokes on 28th November 1929; again, in 1929 the first generation appeared about the beginning of the second week in April, while in 1930 it did not appear until the end of the third week. During the exceptionally cold months of January and February 1929, no *Smynthurus* were obtained in the sweepings, but they were taken in the same months of 1930, although in very small numbers. Such examples serve to illustrate the variability in numbers of *Smynthurus* and in the timing of events in the life-cycle in different years.

2. Method of Rearing.

Observations were made on 50 isolated nymphs reared to maturity in small glass vials. A considerable amount of thought and time was devoted to the development of a suitable technique for the expeditious manipulation and satisfactory rearing of this somewhat delicate and small insect, *Smynthurus* having special requirements, including abundant moisture, a limited range of temperature, soil, etc., for its normal existence; and eventually it was found that the successful rearing of the insect under laboratory conditions was relatively easy of attainment, provided that certain precautions were taken. When specimens had to be dealt with individually, *e.g.*, for growth measurements, it was found most satisfactory to rear each individual separately in a small glass vial, 1 cm. by 4 cm., stoppered with a tight-fitting cork upon which finely sifted soil, moistened with distilled water, was placed. A clover leaf was inserted into the vial and the stalk pressed firmly between the cork and glass, the object of this being to keep the leaf in position, while it also helped to maintain a state of turgidity in the leaf so that it served longer as food for the insect. The tube was placed with the cork downwards, and the soil was kept very moist so that the atmosphere in the vial was almost continually in a state of saturation or very near

it, a very humid atmosphere being one of the essential requirements for *Smynthurus*. Fresh soil and food were supplied as required, which was usually about every fifth day, sometimes every third day, when growth was proceeding rapidly.

3. Number of Instars.

One of the first things which obviously required investigation was the determination of the number of instars and the approximate times spent in the various stadia, as this, so far, was unknown. In the early stages, however, the moulted skins could never be found, or at least, only occasionally, because as was subsequently ascertained from observations, (*a*) the moulted skins are very minute and almost transparent, (*b*) after moulting the insect turns round and proceeds to eat the nymphal exuviae. Recourse was therefore had to the application of Dyar's Law,[5] and this proved an invaluable asset. Accordingly, measurements were made of the width of the head-capsule of 50 nymphs, throughout the various stadia from the first instar to the imago, and the results presented below represent the average of these measurements :—

TABLE I.

Observed width (in micros. units)	Ratio of increase	Theoretical width (as calculated from Dyar's factor)	Instar
1·0	—	—	1st
1·2	1·20	1· 0×1·2—1·20	2nd
1·5	1·25	1· 2×1·2—1·44	3rd
1·8	1·20	1·44×1·2—1·73	4th
2·1	1·17	1·73×1·2—2·08	5th
2·5	1·19	2·08×1·2—2·50	6th
3·0	1·20	2·50×1·2—3·00	7th
3·5	1·17	3·00×1·2—3·60	Imago
	Average ratio of increase—1·197—1·2 (approx.)		

It will be noted that :—

(1) There is an extraordinarily close agreement between the observed and the calculated widths, confirming the applicability of Dyar's Law to a primitive order of insects such as the Collembola (to which order the law has never been applied so far as the writer is aware) as well as to some of the more highly organised orders.

(2) The approximation of the observed to the calculated measurements is sufficiently close to dispose of any doubt as to the possibility of an ecdysis having been overlooked. Hence *S. viridis* undergoes seven moults, there being seven nymphal instars and an imago.

(3) The only marked discrepancy between the actual and theoretical width of the head-capsule is that in the fourth instar, where there is a difference of 0·07 microscopic units or 0·01 mm., actually 4 per cent., which is of no significance when making allowance for the experimental error involved in the measurement of such small dimensions in a live insect.

(4) Each unit in the previous table represents 0·19 mm., so that when converted to actual morphological measurements, the width of the head-capsule in the various instars is as follows :—

Instar ...	1st	2nd	3rd	4th	5th	6th	7th	Imago
Head Width ...	mm. 0·19	mm. 0·23	mm. 0·28	mm. 0·34	mm. 0·39	mm. 0·47	mm. 0·57	mm. 0·66

In describing the first instar nymph, Holdaway remarks that the width of the head is 0·21 mm., so that it seems as if he had overlooked the first instar, and what he actually described was a second instar nymph, the two being very similar except in size, and even in this the difference is very small.

(5) In the measurement of the early instars it was found that a considerable variation exists in the width of the head-capsule, depending upon the time during the interval between successive moults, at which the measurement is made. This is on account of the expansion of the chitin while it is still thin and elastic; in the latter instars it becomes thick and more rigid, so that although the measurements be made at various intervals of time during a stadium, the value for the head-width remains practically constant.

4. Duration of Stadia.

The interval of time necessary for the completion of a stadium depends upon the number of the instar and the influence of environmental factors. At an average temperature of 13° C. (obtained from a continuous chart record) and with optimum conditions of humidity and soil type, the duration of the respective instars is approximately as follows:—

Instar ...	1st	2nd	3rd	4th	5th	6th	7th	Imago
Time in days...	2	3	3	5	5	10	20	15

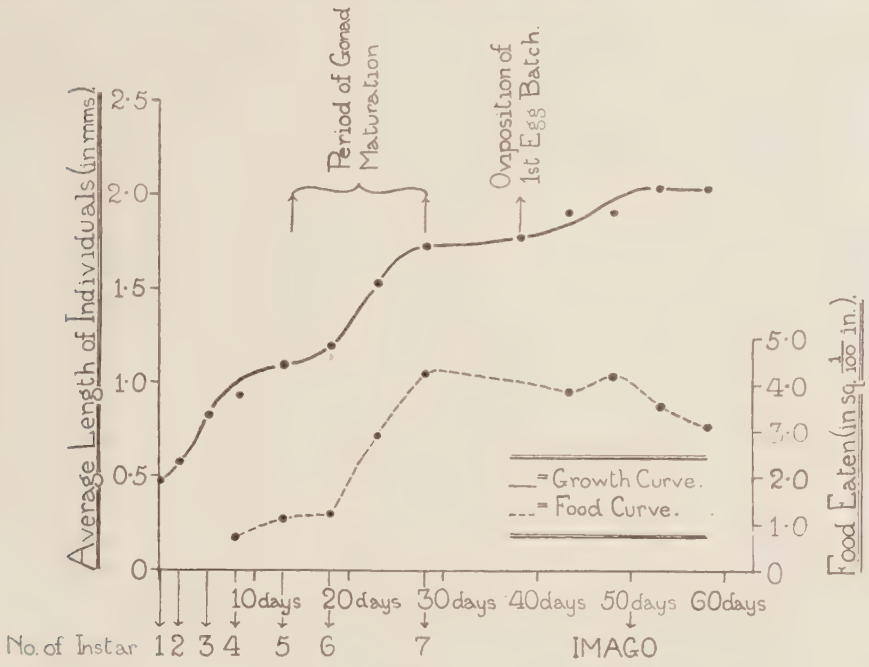
That is, the duration of the life-cycle from the time of hatching to the mature adult is 48 days and the length of life of the imago 15 days, when the individual is subjected to the above-stated environmental conditions.

The developmental period in the egg-stage under the same conditions is about 26 days, making the total duration of the life-cycle, from ovum to imago, approximately two and a half months. There are several points of interest in connection with the above: firstly, the length of the life-cycle is much longer than one would be inclined to anticipate from general observations, taking into consideration also the comparatively small size of the insect; and secondly, the protracted period spent in the seventh instar is worthy of comment. This, however, seems to be due to the fact that sexual maturity is attained in this instar, as numerous individuals oviposited during this stadium, and, as will be observed from the growth curves (*q.v.* subsequent section), the process of oviposition acts as a severe check upon growth. The result is a prolongation in the duration of the seventh instar, and the occurrence of the remarkable and exceptional phenomenon of an ecdysis taking place after the attainment of sexual maturity.

5. Length of Life-cycle.

At higher temperatures there is a rapid speeding up of metabolism, resulting in a much shorter duration of the life-cycle, which, at a mean temperature of 17° C., is now completed in approximately 51 days, where at 13° C., it took 74 days, *i.e.*, an increase of 4° C., produces a decrease in life-cycle duration of 31 per cent. Temperatures over 17° C., however, are not favourable to *Smynthurus*, individuals subjected to such temperatures assuming a pale coloration with a pinched appearance and produce fewer eggs, in marked contrast to the dark-green and rotund forms of

those maintained at lower temperatures. This effect would appear to be due to over-rapid growth, with consequent weakened constitution, resulting in alimentary troubles and the improper functioning of the physiological processes of reproduction.



Graph 1.

6. Growth of Nymphs.

The normal growth curve of *Smynthurus* from first instar to image is presented in Graph I. The point of attainment of the various instars and the amount of food eaten throughout the growth period is also indicated in this graph, so that the relationship of those factors to the complete developmental cycle, and to each other, is visible at a glance. The problem of growth has been studied from various aspects, and a large amount of data concerning the growth of mammals has been accumulated, but very little is known concerning growth phenomena in the lower organisms, including insects. Hence the graph illustrates several features of considerable interest, as follows :—

(1) The growth of *Smynthurus* nymphs is, on the whole, a reasonably smooth and uninterrupted process, but throughout the course of the normal growth curve there can be recognised a series of distinct cyclic variations, each being manifested in the assumption of a sigmoid form by different portions of the complete growth curve. Each cycle consists of three phases, namely, a period of slow growth, followed by a period of rapid growth, and finally a falling-off in the growth rate, and since there are three distinct cycles the total number of phases is nine. Actually, however, the last and the first phases of the first and second and of the second and third cycles, respectively, overlap, making the normal growth curve of the *Smynthurus* nymph a seven phase curve. If the measurements were made at longer intervals, the growth of *Smynthurus* would appear to conform to a single sigmoid curve ; but the measurements were made at intervals sufficiently frequent to avoid this pit-fall, as the graph

adequately illustrates. Hence the problem now before us is the interpretation to be given to the form of growth curve exhibited by this insect.

(2) It will be observed that the first cycle commences immediately after emergence from the egg, the second cycle commences soon after attainment of the fifth instar, and the third cycle approximately mid-way between attainment of the seventh instar and the imago. Now although these recurrent cycles are conveniently indicated with reference to the various stadia, since there is evidently a synchronisation between the initiation of the cycles and the attainment of certain stages in the life-cycle, the primary cause would appear to be the release of certain substances, of a growth promoting nature, at fairly definite intervals throughout the course of development. The graph adequately illustrates the second rapid growth phase which occurs synchronously with the period of gonad maturation, so that we have here something at least analogous to the pre-puberal acceleration of growth which takes place in man. The oviposition of the first batch of eggs marks the initiation of the third and last cycle, but the rate of growth acceleration in this cycle is the least of all three, being most pronounced in the second cycle. The process of oviposition imposes, therefore, a considerable check on growth, the first batch of eggs being deposited by *Smynthurus* before the adult stage is reached, and once this has been accomplished the growth process evidently receives an added stimulus. At temperatures much above 13° C., the cyclic variations in growth are not so apparent, so that although the slope of the curve is steeper, such temperatures have the effect of smoothing out the growth curve on account of their abnormally stimulating effect.

(3) In higher organisms, especially mammals, variations in growth rate have been fairly conclusively associated with the rise and fall in amount of secretions produced by certain ductless glands, such as the thymus, pituitary, etc., but this explanation cannot be applied to insects, for nothing analogous in function to those glands (with the possible exception of the corpora allata and the oenocytes) has as yet been identified in this class. However, further investigations will doubtless reveal in the insect body cells with the capacity to secrete substances associated with growth and various physiological processes (other than digestion), and it has already been shown by Burge[2] that there is a positive correlation between metabolic rate and catalase content. Meanwhile, we must be content with describing the relationship which exists between growth velocity and period of development, and in recognising that whatever the fundamental cause may be, there is a characteristic physiological rhythm underlying the growth process even in such lowly creatures as the Collembola.

(4) As regards the food curve it should first be mentioned that the amount eaten was measured by placing a piece of tracing paper over the clover leaf and marking in the leaf area eaten, the tracing paper being then transferred and placed above squared paper and the shaded areas totalled up. Since the depth of tissue eaten is always approximately the same, namely from one epidermis through to the beginning of the other, it was possible, by supplying leaves of fairly uniform size, to obtain a pretty good idea of the relative amount of food eaten at various stages throughout the growth period. After attainment of the sixth instar there is a very marked rise in the amount of food eaten, corresponding with the rapid acceleration of growth in the second cycle, after which there is a slight falling off, followed by a second maximum, corresponding with the middle of the last growth-cycle, and the attainment of the imago. Subsequent to this there is a gradual reduction in the amount of food eaten, corresponding with the onset of senescence. From the point of view of damage done, while this will, of course, depend primarily upon the density of population, the injury caused by the individual up to the end of the fifth instar is relatively insignificant compared with that of the three last stages.

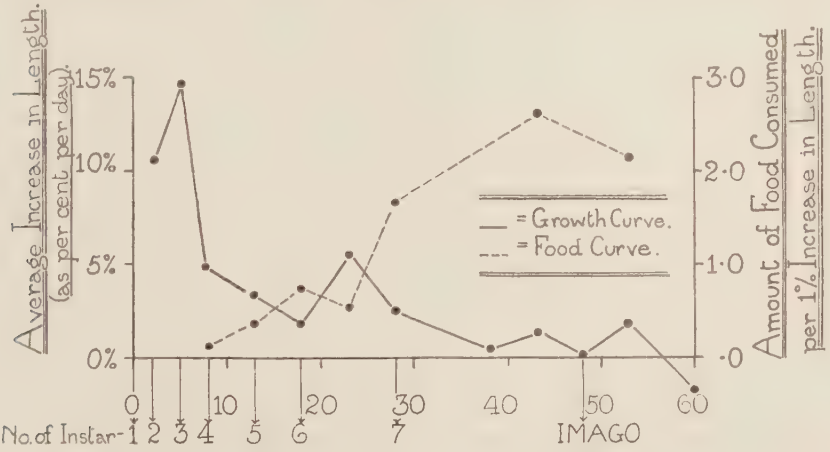
In the previous graph there was demonstrated the *absolute* growth rate and the total amount of food eaten at various intervals throughout development, but this

gives no indication of the *relative* growth rate (*i.e.*, the increment of growth in proportion to the size already attained) or the amount of food eaten in relation to bodily size. Graph 2 has, therefore, been constructed to illustrate these relations. The data used in the construction of both Graphs 1 and 2 are presented below in tabular form.

TABLE II.

Average length (in micro. units)	2·51	3·0	4·35	4·97	5·8	6·35	8·05	9·05	9·55	10·05	10·05	10·9	10·8
Average length in mm. (one micro. unit = 0·19 mm.) ...	0·47	0·57	0·82	0·94	1·10	1·20	1·53	1·72	1·78	1·91	1·91	2·07	2·05
Food consumed (in sq. 1/100 in.)	—	—	—	0·70	1·11	1·19	2·85	4·21	—	3·85	4·20	3·55	—
Average increase in length (as per cent. per diem)	—	10·6	14·6	4·9	3·4	1·8	5·5	2·5	0·35	1·46	0·0	1·67	1·9
Food consumed per 1 per cent. increase in length (in sq. 1/100 in.) ...	—	—	—	0·14	0·32	0·66	0·52	1·68	—	2·64	—	2·12	—
No. of instar ...	1	2	3	4	5	6	-	7			8	-	--
Time in days ...	0	2	5	8	13	18	23	28	38	43	48	53	58

The growth curve presented in Graph 2 represents the average increase in length per diem expressed as a percentage of the size already attained. The graph illustrates the very rapid falling off in relative growth rate which occurs after the attainment



Graph 2.

of the third instar, followed by a more gradual decrease with increasing age, but punctuated as it were by spurts of growth corresponding with the mid-point in each growth-cycle. This means that the rate of tissue formation is greatest during a period which

represents approximately the initial 10 per cent. of the total growth phase. On the other hand the amount of food consumed for every 1 per cent. increase in length increases rapidly with age, the relationship being roughly linear in character, with the exception of the periods of most rapid growth in each cycle, during which the insect is either capable of deriving a greater energy value from its food or of utilising that energy in the process of tissue formation more efficiently, such as might be provided by the periodic stimulation of enzyme secretion.

7. Oviposition.

During the seventh instar the nymphs become sexually mature and the first batch of eggs is laid. Macnamara[15] states that an English writer who had studied Collembola for 50 years had never succeeded in observing oviposition, but a detailed account of the process in *Smynthurus viridis* has been given both by Holdaway and Davies, and indeed may be observed without difficulty in *Smynthurus* throughout the egg-laying period. On account of its somewhat unusual nature the oviposition process will be briefly described here to enable the reader to obtain a connected account of the present investigation. The female, having chosen a suitable spot for oviposition (and, as will be shown later, the female does exhibit a selective action in this respect) depresses her head and raises the end of the abdomen. Soon after this a yellow mass exudes from the reproductive opening and gradually assumes a spherical form. The insect remains in this position for a few moments and a mixture of earth and excrement from the anal opening gradually envelopes the egg, which is worked round by a circular movement of the end of the abdomen and pressed firmly on to the soil thereby. The whole process requires about three minutes. Oviposition in this insect is therefore a somewhat lengthy process on account of the necessity of consuming sufficient soil to act as a coating for each egg, and judging from its effect upon growth is also of a very exhausting character.

The eggs are arranged in the form of a dome-shaped mass, and as the result of numerous observations the writer found the average number of eggs in each batch to be about 30–35, but varying by as much as 3–100, according as conditions are favourable or otherwise. The maximum number of eggs laid by an individual, under optimum conditions, is about 120. Egg-laying commences in the seventh instar, at a mean temperature of 13° C. and relative humidity almost 100 per cent., and usually takes place 30–35 days after emergence. As will be shown later, however, these conditions are not the optimum for oviposition in *Smynthurus*. A second batch of eggs may be laid at an interval of about 10 days after the first, but this interval may vary from 8 to 14 days, and in some instances a third batch of eggs is laid. Out of 20 females which deposited a first batch of eggs, 10 deposited a second batch, and 3 a third; the number of eggs in each batch, however, was very different. Generally, the second egg-batch contains nearly 50 per cent. more eggs than the first, a fact which is doubtless due to the smaller size and relative immaturity of the individuals when the first egg-batch is deposited, as compared with the full-grown adults which deposit the second batch. The third egg-batch varies very considerably in size, but usually contains about 33 per cent. of the number of eggs in the first batch, and is deposited (by about 15 per cent. of ovipositing females) after the second batch at an interval which varies widely but averages about 8 days.

In order that oviposition by *Smynthurus* may proceed normally there must be present in the environment a certain combination of factors, and the absence of any one of these causes a profound reduction in the number of eggs laid. The essential factors are (*a*) low temperatures, (*b*) high relative humidity, and (*c*) soil of a suitable chemical and mechanical constitution; but all these factors will be treated in detail in a subsequent section. Suffice it to say for the present that the demands of this

physiological process upon the environment are more exacting than those of any other phase of development, and hence the period of oviposition may be aptly termed the critical phase in the life-cycle.

8. Hatching.

The egg is spherical, smooth, and pale yellow in colour, being 0·25 mm. in diameter when deposited. The eggs are laid at the base of herbage, on the soil surface, and on account of the coating of soil are rendered extremely difficult of discovery in the field. Holdaway suggested that the coating of soil round the egg assisted hatching by distributing moisture over the egg surface, and though this is highly probable, the significance of this phenomenon might be worthy of investigation. It certainly would appear that the coating of soil affords a considerable measure of protection against other animals, including insect larvae and adults, whose mode of living consists of scavenging along the soil surface amongst the layer of decaying vegetable matter and organic débris, which tends to accumulate there.

Just before hatching a slight elongation in a direction corresponding to the longitudinal axis of the embryonic nymph takes place, and this is followed by a circular splitting of the chorion slightly towards the anterior end. There being nothing in the nature of hatching spines or any other device for the specific purpose of facilitating eclosion, the latter takes place by means of body movements of the embryonic nymph, presumably assisted by the purely mechanical effects resulting from fluctuations in the physical factors of the environment. When development of the embryonic nymph has proceeded to about 80 per cent. of completion, the eyes and antennae become clearly visible through the chorion, and so afford a valuable criterion as to degree of development. Hence in the course of laboratory experimentation, such as the effect of temperature upon speed of development of the egg, the appearance of the eyes, in the form of two black dots shining through the chorion, acts as a warning of the approach of developmental completion, so that from the time of their appearance the careful investigator will increase the frequency of his observations, if it is desired to determine the time of eclosion with any degree of accuracy.

The time required for hatching to occur varies tremendously, depending upon environmental conditions, of which by far the most important are temperature and humidity. No matter what the temperature may be, unless the substratum upon which the eggs are placed is kept continually saturated with moisture, or the eggs be maintained in an atmosphere of 100 per cent. R.H., when this is their only source of moisture, hatching will not take place. On the other hand, if excessive moisture is supplied so that a film of water is continually maintained on the surface of the egg (and on account of capillarity there is a tendency for this to occur on a moisture-laden substratum), the result is delayed or totally inhibited development, depending upon the thickness of the film, on account of deprivation of oxygen. Given suitable conditions of temperature and moisture, *i.e.*, about 14–16° C., and a saturated atmosphere, hatching occurs in 19 days. Development still proceeds normally, and with increasing speed, up to 21° C., while below 9° C., development proceeds exceedingly slowly and is almost inhibited below 7° C.

9. Sex Ratio.

The disparity in the numerical relative production of the sexes is very marked, and seems worthy of comment before bringing this study of the life-history to a close. Out of 30 third instar nymphs taken from the insectary at random, and reared singly in small glass vials under laboratory conditions, 25 attained to sexual maturity and 20 laid eggs. Again, out of 70 last instar nymphs and adults taken at random from

the field and kept isolated in the laboratory, no less than 58 laid eggs, the remainder dying off without laying any eggs, and hence being, presumably, males. The latter appear to be more abundant in late autumn than during the summer, when higher temperatures prevail, so that the production of males appears to be associated with certain environmental conditions. In any case the sex-ratio (tertiary) is remarkably low, being 22 : 100 (approximately) when expressed as the number of males per 100 females, and this inequality in numerical proportions is not due (at least entirely) to a differential sex mortality.

10. The Significance of Life-history Studies.

At one time it was thought that a knowledge of the life-cycle of an insect pest was sufficient to ensure its speedy elimination, the object being to break the weakest link in the biological chain. Entomologists, however, are beginning to realise that a greater breadth of outlook is required on the whole problem of insect abundance, and that a knowledge of the life-history is merely a preliminary to a proper understanding of the species in relation to its surroundings, both animate and inanimate.

This idea of the relationship between the organism and its environment assumes greater significance in the study of insect control, the more it is realised that the life as lived in Nature is an expression of the reaction of the organism to its environment, and that different factors in the environmental complex call forth different responses on the part of the organism. Man, being a mammal, is provided with a regulating mechanism which tends to stabilise his internal environment and to render him, to a certain extent, indifferent to external changes, whereas in the case of invertebrates changes in temperature, humidity, barometric pressure, acidity, electrical state, etc., may have a profound significance.

It is this instability of environmental factors (resulting in many cases from a deliberate alteration of the environment by man in growing his crops) which is in large measure responsible for the abnormal variations in the numbers of animals, known as "plagues." Accordingly, an attempt has been made below to analyse quantitatively the effect of the various environmental factors, biotic and physical, which contribute towards checking the normal increase in the numbers of *Smynthurus* under conditions existing in this country, where the population is evidently stabilised. By this means it has been possible to determine the factors which are effective in stabilising the *Smynthurus* population, and so to account for the fact that in one environment the insect may be present in numbers of negligible economic significance, while in another the population may attain sufficient proportions to assume the characteristics of a "plague" and become a menace to man's welfare.

III. The Method of Investigating Environmental Factors.

In regard to the difficulties involved in an investigation of this kind, one of the most serious is due to the fact that there are few methods for obtaining quickly and easily an accurate quantitative sample of the numbers and kinds of organisms; secondly, on account of the multiplicity of factors acting simultaneously in nature, the effective action of any single factor is rendered very difficult of assessment. In regard to the method adopted the writer has attempted to steer a middle course between two extremes, or rather, to effect a judicious combination of these, in recognition of the fact that there are two distinct methods available in studying the factors of insect control :—

(*a*) By means of accurately controlled experimentation in the laboratory involving the use of sensitive apparatus, to create a known environment, and observe the effect it produces.

(*b*) By means of field observations, involving the use of quantitative estimates of the population, to attempt an analysis of the environment by the correlation of fluctuations in the population with meteorological phenomena.

Both methods have their disadvantages, the most serious objection to the first being the high cost of apparatus sufficiently sensitive to obtain accurate control of the environmental factors which it is desired to vary; secondly, despite the obvious advantages of controlled experimentation in the laboratory, when their object is to explain the population variations in a natural environment, the results will only hold good in so far as they approach the conditions obtaining in nature. The second method is an empirical one, and it is frequently hard to distinguish between primary and secondary effects. An additional complication results from the inter-relationship of external factors such as temperature and humidity, so that the effect produced may not be entirely a function of a single factor, but dependent, to a certain extent, on the intensity of action of some other factor in the environment. This, of course, also constitutes an additional complication in the first method. In studying the factors of insect control, therefore, the writer is of opinion that (i) the two methods are complementary and that the first must act as a reinforcement to the second; (ii) in order to get a proper understanding of the fundamental principles governing insect abundance, distribution, and control, that the correct method of procedure is to correlate the results of quantitative field observations with those obtained from critically planned and controlled experimentation in the laboratory, *i.e.*, by a judicious combination of the methods of the experimental entomologist and the animal ecologist.

Having obtained a fairly complete account of the life-history of the springtail, including a detailed examination of the various stadia, number of instars, growth rate, etc., under controlled conditions of temperature, humidity, and soil type, the next appropriate step in the investigation appeared to be the collection of quantitative field observations. These included a fortnightly record of the seasonal distribution of *Smynthurus* on pastures of different types, and in the outdoor insectary, where conditions of temperature and humidity were somewhat different from outside, but were accurately recorded on instruments for the purpose; also a monthly census of the entire insect population in those fields where records of the fluctuations in the *Smynthurus* population were being made, the object of the latter being to determine whether there was any evidence of a correlation between the variation in the level of the population and the fluctuations of biotic factors in the environment.

The necessary field data having been obtained, the next advance in the investigation consisted in the accumulation of accurate quantitative evidence as to the effect of various environmental factors, which, as ascertained by an analysis of the field data, were obviously influencing the natural activities of the insect, but could only be correlated with these in a semi-empirical manner. For instance, the fact of a high negative correlation between the size of the *Smynthurus* population and the atmometric index can only be explained scientifically by a careful analysis of the effect of the several factors influencing the atmometric index upon those vital activities which contribute towards the physiological make-up of the individual in all its phases, from the formation of the ovum till death. Hence this section of the paper contains an account of the activities of the investigator as transferred from the field to the laboratory, with a view to substantiating the evidence obtained from field data, by means of quantitative results derived from controlled experimentation in the laboratory. The reader must bear in mind that, although the account of the laboratory experiments is presented before the field data, they were actually undertaken as the result of suggestions derived from an analysis of the latter, the object being to facilitate the explanation of the fluctuations in the *Smynthurus* population, since the latter are due to the simultaneous action of several factors, and will be more readily appreciated by the reader with some previous knowledge of the effect of environmental factors upon the physiological processes of *Smynthurus*. The

majority of the experiments, therefore, were conducted with a view to ascertaining how the various environmental factors, both biotic and physical, might operate in checking the increase of the *Smynthurus* population, and recording this effect quantitatively.

Now it is the belief of the writer that the effective action of any environmental factor in limiting the size of a natural population may come into operation in two different ways, although, of course, this does not preclude the simultaneous action of that factor in either manner ; firstly, the effect of that factor upon the actual number of individuals, and secondly, the effect of that factor upon the potential number of individuals. The former is obvious, *e.g.*, the action of parasites and predators as biotic factors of control, and the effects of physical factors such as abnormal heat or cold, dessication, etc., upon the various stages in the life-cycle of insects and other animals, as well as plants. The latter is less obvious and has thus, perhaps, not received the attention it merits, although increasing examples of this effect are gradually becoming known, *e.g.*, " twinning " in sheep has been correlated with the absence of rainy days during the rutting period (Nichols[16]), and the number of eggs shed at each heat period in the rabbit is dependent on climatic conditions during the breeding season (Hammond[9]). The effect of an environmental factor upon the potential number of individuals also includes the action of biotic factors, *e.g.*, the " parasitic castration " of certain bees of the genus *Andrena* by *Stylops*, *Typhlocyba* by *Chalarus*, the nematode *Sphaerularia* in queen bees of *Bombus*, etc., while the more subtle and as yet hardly examined effect of the presence of one individual upon another of the same species, and which in the present imperfect state of our knowledge must be termed " psychological," is also referable to this category.

Since (i) the action of an environmental factor upon the potential number of individuals is brought about through its effect upon the adult of the preceding generation (and perhaps in some cases upon the grandparent), and (ii) the size of a population at any time represents the difference between the birth rate and the death rate—it follows that experiments conducted with the object of explaining the size of a population in terms of the inhibiting and decimating effect of environment upon the potential and actual numbers of individuals, respectively, must be largely concentrated on the effect of environmental factors upon (*a*) growth, (*b*) fecundity, (*c*) longevity. Accordingly, the results are given of a series of laboratory experiments dealing largely with various environmental effects upon these three vital characteristics. In addition to the above there must also be taken into consideration (*d*) survival in the presence of enemies, *i.e.*, the influence of biotic factors. The latter will be considered first.

IV. Effect of Biotic Environmental Factors upon Survival.

From time to time, throughout the progress of the work, insects and arachnids appeared in the sweepings from France and the collections at Farnham Royal, which suggested the probability of their being predators upon *Smynthurus*. In order to test the probability of any insect or arachnid being a predator, a series of laboratory feeding tests were conducted. These simply consisted of transferring the supposed predator to a clean glass vial of suitable size, and feeding it with *Smynthurus* adults or nymphs. A note was made of the locality in which the likely predator was taken, the number of days it remained alive in captivity, and the total number of *Smynthurus* consumed during that period. Having accumulated information of this type for a considerable number of insects and spiders, a problem arose in regard to the correct basis for calculating predatory efficiency. Obviously, the average number of *Smynthurus* eaten daily does not alone convey an accurate idea of the predatory value of a species, since it gives no idea of the total number consumed during the life-cycle.

TABLE III.—*Insect Predators of* Smynthurus viridis (*Linn.*).

Name	Period in captivity	Days in captivity	No. Smynth. eaten	Av. No. Smynth. eaten daily	Grade of Predatory Efficiency	
					No. 1 Criterion	No. 2 Criterion
COCCINELLIDAE.						
Coccinella sp.	25th Sept.—17th Oct.	22	40	1·8	Fairly good predator	—
C. undecimpunctata, L.	20th Sept.—19th Oct.	29	50	1·7	Fairly good predator	—
C. septempunctata, L....	23rd Oct.—10th Dec.	48	70	1·5	Good predator	Fairly good predator
C. septempunctata, L....	8th Apr.—10th June	63	170	2·7	Good predator	Good predator
Larva of *C. 7-punctata*	24th Apr.—14th May	20	20	1·0	—	—
STAPHYLINIDAE.						
Philonthus politus, F....	26th Sept.—17th Oct.	21	60	2·9	Fairly good predator	Fairly good predator
P. laminatus, Creutz.	27th May—5th June	9	70	7·7	—	Fairly good predator
Stenus cicindeloides, Sch.	29th Sept.—13th Nov.	45	62	1·4	Good predator	Fairly good predator
S. similis, Herbst	10th May—20th May	10	30	3·0	—	—
Lathrobium brunnipes, F.	27th Oct.—3rd Dec.	37	95	2·6	Good predator	Good predator
Paederus littoralis, Grav.	10th May—27th May	17	60	3·5	—	Fairly good predator
P. littoralis, Grav. (2)	1st June—15th Aug.	75	419	2·8	Good predator	Good predator
Xantholinus linearis, Ol.	11th Oct.—22nd Oct.	11	40	3·6	—	—
CARABIDAE.						
Bembidium littorale, Cl.	27th Oct.—7th Nov.	11	20	1·8	—	—
TELEPHORIDAE.						
Cyrtosus cyanipennis, Er.	2nd May—1st June	30	100	3·3	Fairly good predator	Good predator
ANTHOCORIDAE.						
Anthocoris nemorum, Linn.	5th Oct.—9th Oct.	4	10	2·5		—
CAPSIDAE.						
Lygus pratensis, Linn.	11th Oct.—15th Oct.	4	20	5·0	—	—
FORFICULIDAE.						
Forficula auricularia, Linn. (2 ♀) ...	24th Sept.—12th Dec.	79	958	6·0	Good predator	Good predator
F. auricularia, Linn. (♂)	1st Nov.—5th Dec.	34	195	5·7	Fairly good predator	Good predator

However, when taken in conjunction with the number of days over which the average consumption was obtained, it acts as a valuable criterion of predatory efficiency. The total number of *Smynthurus* eaten is undoubtedly the best single index for assessing the value of a predator. Eventually it was decided to use two criteria as follows :—

(1). (*a*) Average number of not less than 1·4 *Smynthurus* eaten daily, and no fewer than 35 days in captivity—" Good predator."

(*b*) Average number of not less than 1·4 *Smynthurus* eaten daily, and no fewer than 21 days in captivity—" Fairly good predator."

(2). (*a*) Total consumption during captivity of not less than 90 *Smynthurus*—" Good predator."

(*b*) Total consumption of not less than 60 *Smynthurus* during captivity—" Fairly good predator."

The list of insect and spider predators, with data pertaining thereto, is presented in tabular form (see Tables III and IV respectively), from which it will be observed that these two criteria of predatory efficiency are in complete agreement in all important respects, the most important differences being in the fact that in No. 2, *Stenus cicindeloides* and *Evophrys* sp. drop out of the " good predators " and *Cyrtosus cyanipennis* moves into them. According to No. 1 there are thirteen different species of good predators and six fairly good predators, whereas according to No. 2 there are twelve different species of good predators and six fairly good predators, both spiders and insects being judged on the same standards of efficiency. From an examination of the data in Tables III and IV it is fairly evident that all species listed as good or fairly good predators must, when considered collectively, exert at least a significant degree of control. Meanwhile we can proceed to an examination in greater detail of the individual predators, with the object of attempting to throw further light on their predatory significance by a consideration of their geographical distribution, habits, life-history, etc. In this way it becomes possible to focus attention upon the similarities or discrepancies existing in the ecological peculiarities of the different species, and thus obtain a view of the relationship between prey and predator in its proper environmental perspective.

1. Insect Predators.

Coccinella septempunctata, L.

This common species of Ladybird, well known as a devourer of Aphids and Coccids, proved itself capable of taking to a *Smynthurus* diet with considerable avidity, and of living on nothing but *Smynthurus* adults for as long as nine weeks, in one particular instance. That *C. septempunctata* would live on *Smynthurus* was not altogether unexpected, since this species exhibits considerable catholicity of taste in that it is predacious upon larvae of the vine moths, *Clysia ambiguella*, Hb., and *Polychrosis botrana*, Schiff., in France, upon the Psyllid, *Trioza viridula*, in Latvia, upon Coccids in Palestine, and has been shown to take the eggs and larvae of *Pyrausta nubilalis*, Hb., in Germany. Smee found that the adults ate small froghopper nymphs as well as Aphids when kept in captivity. Whether these different species contribute towards a variation of the daily menu or simply act as stop-gaps in times of Aphid scarcity is not exactly known, but in the case of *Smynthurus viridis* at least, there exists a potential source of food supply which is presumably utilised. Since *C. septempunctata* is common throughout Britain and the Continent and the adults (of different generations) are active from the end of April till the beginning of October, the seasonal and geographical range of activity in Europe of *C. septempunctata* and *Smynthurus viridis* exhibit a considerable degree of similarity.

Coccinella septempunctata larvae were much less inclined to accept *Smynthurus* as food than the adults, but this may have been partly due to the fact that the larvae used in the feeding tests were fairly well grown, and commenced to pupate after 10–20 days in captivity.

Coccinella undecimpunctata, L.

This species of Ladybird also proved its capacity to take *Smynthurus*, but not with the same avidity as its 7-spotted relative. It is also a great devourer of Aphids, and has been reported as predacious on *Aphis sorghi* in the Anglo-Egyptian Sudan. The variation in the menu would appear to be somewhat more restricted than that of *C. septempunctata*.

Philonthus politus, F.

This beetle attacked and devoured *Smynthurus* without any hesitation when the latter were placed in the experimental feeding vial, and although it lived for only three weeks in captivity, the average number of *Smynthurus* eaten daily was fairly high. *P. politus* is found in vegetable débris, moss, etc., and has a wide distribution, being found over the Palaearctic and Nearctic regions, Tasmania, and New Zealand, according to the "Coleopterorum Catalogus" of Junk & Schenkling.[12] Here again we have areas which are at least climatically favourable for a considerable portion of the year to both species, as will be shown subsequently in this paper.

Philonthus laminatus, Creutz.

This species of *Philonthus* proved to be a slightly more efficient predator than the previous one. It, also, is common and widely distributed throughout Britain and the Continent, particularly in the Mediterranean region.

Stenus cicindeloides, Grav.

It soon became evident that this species required fairly moist conditions for survival, so sterilised soil was added to the feeding vial and maintained in a moist condition. The beetle was observed on several occasions in the act of catching and devouring its prey, which it sought with considerable agility. According to Fowler,[7] *S. cicindeloides* is common and generally distributed in the London, South, and Midland districts of England, being rarer further North, and in Scotland confined to the Solway district. On the Continent, it is found over Europe, in Siberia, and in Madeira, always preferring moist, shady situations such as obtain among the roots of tall grass and among mosses, etc.

Stenus similis, Herbst.

This species was not supplied with moist soil, and this perhaps contributed to its relatively short life in captivity, as it was observed with most species of *Stenus* that they lived much longer when maintained on a soil substratum kept well moistened with water, although, according to Fowler,[7] *S. similis* is usually found in comparatively dry places, in marked contrast to the previous species. Both *S. cicindeloides* and *S. similis* belong, however, to the group of the genus *Stenus* which is characterised by having a bilobed penultimate tarsal joint, which is supposed to facilitate their clinging to plant stems. *S. similis* is quite common throughout Britain and the Continent of Europe, particularly in the Mediterranean region.

Lathrobium brunnipes, F.

This Staphylinid proved itself a great devourer of *Smynthurus*, "cleaning up" the victims almost entirely, so that nothing but a few scattered pieces of chitinous integument remained after the completion of a meal. According to Fowler,[7] the

genus *Lathrobium* is a large one, but is chiefly confined to the temperate and cold regions of the earth, again coinciding very well with the approximate distribution of *Smynthurus*. *Lathrobium brunnipes* is common throughout Britain, northern and middle Europe, and Siberia, always preferring comparatively shady situations.

Paederus littoralis, Grav.

This brightly coloured Staphylinid is easily placed amongst the best predators of *Smynthurus viridis*. Chasing its prey with great agility and seizing the unfortunate victim in its powerful jaws, *Paederus littoralis* soon disposes of the *Smynthurus*, whether nymphs or adults, although the former would appear to be preferred, presumably because they are younger and more palatable. It is not improbable that the noxious agent which appears to be present in the body fluids of *Smynthurus*, judging from the conduct of certain ants and other species, is present in the nymphs in a less highly concentrated form, rendering them less distasteful, so that some species which will not countenance an adult will sample nymphs without much reluctance. Specimens of *Paederus littoralis* used in these feeding tests were all taken from different localities in France, although the species is well known in England from the midland counties southwards, being exceedingly common, according to Fowler[7], in the South of England. The genus is best represented in the Tropics, but a dozen species are found in Europe, inhabiting the roots of grass in damp, marshy situations—a very favourable habitat for *Smynthurus viridis*.

Xantholinus linearis, Ol.

This species is undoubtedly a slightly better predator than the data would appear to make it on account of its short period in captivity. Several other species of *Xantholinus* are very good predators, *e.g.*, *X. cephalus* on *Ips pini* in America, and *X. hamatus* on *Chortophila brassicae* in Canada. According to Junk & Schenkling.[12] *Xantholinus linearis* is known throughout the Palaearctic region.

Bembidium littorale, Ol.

In the list of *Smynthurus* predators this is the only representative of the CARABIDAE, and it is a more efficient predator than the data would appear to make out, and for a similar reason to that given for the previous species. The *Smynthurus* were devoured almost entirely, there being nothing left in the feeding vial but a few chewed up fragments of chitinous integument. The species of *Bembidium* are largely confined to the temperate regions of the Northern Hemisphere, and are typically inhabitants of damp, marshy places. In his "Genera des Coléoptères d'Europe," Jacquelin du Val[11] remarks "les Bembidium sont des insectes généralement petits et extrêmement agiles; ils aiment pour la plupart les lieux humides, le bord des eaux courantes, et se cachent sous les pierres, les détritus, etc." The reader will observe that the morphological characteristics and ecological relationships contribute much towards the likelihood of this species being a fairly constant predator of *Smynthurus*. Other species are known to be good predators, *e.g.*, *B. lampros* on gravid females of *Longitarsus parvulus*, Payk., and *B. mutatum* on *Chortophila brassicae*.

Cyrtosus cyanipennis, Er.

This voracious devourer of *Smynthurus* was maintained in captivity for 30 days, after which it escaped from the vial while being fed and could not be recovered, despite an exhaustive search. It is the only member of the TELEPHORIDAE (a large family with numerous carnivorous species) represented in the list of *Smynthurus* predators. Specimens were received from: Hyères, in the South of France, this species being apparently more or less confined to the Mediterranean regions of Spain, Italy, and France, although extending further north in the case of the latter country.

TABLE IV.—*Spider predators of* Smynthurus viridis (*Linn.*).

Name	Period in captivity	Days in captivity	No. Smynth. eaten	Av. no. of Smynth. eaten daily	Grade of efficiency	
					No. 1 Criterion	No. 2 Criterion
THOMISIDAE.						
Philodromus sp. (immature)... ...	5th Oct.—26th Nov.	52	100	1·9	Good predator	Good predator
Xysticus sp. (immature)	14th Sept.—23rd Nov.	70	120	1·7	Good predator	Good predator
Tibellus oblongus, Wal.	26th Sept.—17th Dec.	82	140	1·7	Good predator	Good predator
LINYPHIIDAE.						
Erigone sp.	10th May—21st June	42	100	2·4	Good predator	Good predator
Trachygnatha dentata, Wid. ...	14th Sept.—25th Sept.	11	5	0·5	—	—
Lephthyphantes zimmermannii, Bertk.	5th Oct.—17th Dec.	73	110	1·5	Good predator	Good predator
EPEIRIDAE.						
Meta segmentata, Clerck (immature)	5th Oct.—27th Dec.	22	50	2·3	Fairly good predator	—
Meta segmentata, Clerck	5th Oct.—27th Nov.	53	90	1·7	Good predator	Good predator
Epeira umbratica, Clerck	11th Oct.—13th Nov.	33	40	1·3	—	—
Pachygnatha degeerii, Sund.	11th Oct.—7th Dec.	37	90	1·6	Good predator	Good predator
Singa hamata	22nd Nov.—3rd Dec.	11	10	0·9	—	—
SALTICIDAE.						
Evophrys sp. (immature)	8th Apr.—28th May	50	70	1·4	Good predator	Fairly good predator

NOTE.—No. 1 *Criterion of predatory efficiency.*

(i) Average number of not less than 1·4 *Smynthurus* eaten daily and no fewer than 35 days in captivity—"Good predator."

(ii) Average number of not less than 1·4 *Smynthurus* eaten daily and no fewer than 21 days in captivity—"Fairly good predator."

No. 2 *Criterion of predatory efficiency.*

(i) Total consumption during captivity of not less than 90 *Smynthurus*—"Good predator."

(ii) Total consumption during captivity of not less than 60 *Smynthurus*—"Fairly good predator."

Anthocoris nemorum, L.

The bug was observed with its victims impaled on its proboscis. Butler,[3] quoting Bold, says it is a great devourer of aphides, and doubtless the latter will normally fall a much easier victim than the saltatory *Smynthurus*, although there is little chance of escape when confined in a small glass vial. However, this species is undoubtedly carnivorous, and being very common and widely distributed, will doubtless include *Smynthurus* occasionally in the menu. According to Oshanin,[17] the distribution of *A. nemorum* includes the whole of Europe, Algeria, Egypt, Asia Minor, Caucasia, and Siberia, so that it not only occupies the geographical territory of *Smynthurus* but extends somewhat beyond it. The bug is found on numerous shrubs and low plants.

Lygus pratensis, L.

This Capsid sucked the juices of its *Smynthurus* victims fairly well, but the remarks made in regard to the previous species, in its relationship to *Smynthurus*, also apply to a large extent in this instance. The remarks of Butler[3] may be quoted in this respect; "this is one of the most widely distributed species in the whole of the CAPSIDAE, occurring over the entire Palaearctic region, and over the American Continent as far South as Mexico and Guatemala. It is a species which is evidently possessed of great plasticity, as is shown by its great variability, its wide geographical range, and its great variety of host-plants. If, as appears probable, it is a carnivore as well as a vegetarian in diet, this would be further evidence of its adaptability and a guarantee of its survival."

Forficula auricularia, L.

The common European earwig proved to be one of the most voracious of all the *Smynthurus* predators, the females having a greater appetite than the males. Two females ate no less than 958 *Smynthurus* in 79 days, after which no food was supplied, and they died on the 59th and 60th days, respectively, subsequent to this. The average daily food requirement for a female earwig is about six *Smynthurus*, that of the male being about 5·7. Much has been written about the food of the European earwig, and it is now recognised as an omnivorous species, sometimes wreaking havoc amongst the gardener's ornamental plants and vegetables and sometimes eating up his insect enemies. Although it is generally recognised among entomologists that the evil reputation of the earwig is only partly merited, never before have Collembola been listed in its menu. After some time in captivity the earwigs became extremely fond of the *Smynthurus* diet and darted about the container in pursuit of their prey with the utmost agility, although they never required any persuasion to accept this form of food.

2. Spider Predators.

Since it was not possible to determine the species of some of the spider predators on account of their immaturity, these cannot be treated in such detail as the individuals which have been determined specifically. However, in the case of spiders this is not of very much significance since their food habits are not, as a rule, peculiar to any single species, the class exhibiting such catholicity of taste. Further, in regard to general ecological relationships whole genera, and even families, exhibit a considerable homogeneity.

Philodromus sp. (immature).

This spider was taken amongst *Smynthurus* on clover in the outdoor insectary, and like the other two Thomisid spiders (all of different genera) proved a great devourer of the Collembola. THOMISIDAE exhibit the familiar phenomenon of

protective resemblance, *Xysticus* (the following genus, lurking among fallen leaves, while *Philodromus*, on account of its more elongated form, is better designed to obtain invisibility along grass-stems, whence it pounces upon the unsuspecting prey.

Xysticus sp. (immature).

This is a large genus of crab-spiders which live under stones or loose bark and at the roots of plants. They are of a brownish-fawn colour with a characteristic pattern on the cephalothorax, so that they are easily recognised, the species *cristatus* being very common and widely distributed. During 70 days in captivity this individual ate no less than 120 *Smynthurus*, of which nothing was left but the dried-out and shrivelled exoskeletons.

Tibellus oblongus, Wal.

Of all the Thomisids predatory upon *Smynthurus viridis* this species was perhaps the best. It is an exceedingly active creature, with a long and slender body, upon which are three long and tapering brown stripes, making it a difficult object to perceive amongst semi-decayed grass stems. The species is a very common one and is particularly abundant in marshy localities in the South of England. Besides Europe and Asia, it is found throughout the United States of America and in Alaska.

Erigone sp.

This specimen was taken in the vicinity of the laboratory on 10th May from a field in which *Smynthurus* was very abundant, and despite its small size this individual devoured no less than 100 *Smynthurus* within 42 days. The disembowelled corpses were placed in a neat pile in a corner of the vial. The characteristic habitat of the genus is among grass roots and low herbage, and on account of their small size and secluded lives they seldom attract attention. Nevertheless, they are very abundant in Britain during the early summer and late autumn. In a private communication, Mr. Bristowe informs the writer that on calm, sunny days in October and November they represent, as a rule, at least 50 per cent. of the small black spiders which migrate at that time of the year. Numerous specimens of the two Erigonid species, *atra*, and *dentipalpis*, were observed in the same field during the month of November. Dr. Myers also observed that species of *Erigone* were predacious upon these Collembola.

Trachygnatha dentata, Wid.

Although a poor predator, judging from the data presented, this species is, perhaps, considerably better than it would appear to be, as it did not remain alive in captivity long enough to be subjected to a proper test. It is largely restricted to marshy ground or damp herbage.

Lephthyphantes zimmermannii, Bertk.

This Linyphiid was taken in the outdoor insectary at Farnham Royal in which *Smynthurus* were being reared on white clover, and it proved to be extremely fond of this form of food, devouring 110 *Smynthurus* within 73 days. The species belongs to the section Linyphiales of the family LINYPHIIDAE, that is to say, their activities are pursued on a slightly higher level than the ground-loving Erigonales. *L. zimmermannii* builds a flimsy sheet-web at the roots of grasses and other herbage.

Meta segmentata, Clerck (immature).

This genus, together with the three following ones, are included in the family EPEIRIDAE, the mostly highly specialised of all spiders. According to Savory,[18] *Meta segmentata* is the most numerous of British spiders, and from spring to autumn may

be found on almost every bush. Moreover, it is one of the few spiders that produce two broods in one year. Specimens were taken in *Smynthurus* sweepings from both France and England, and when fed in captivity accepted the insects with great avidity.

Epeira umbratica, Clerck.

The spider was taken in the *Smynthurus* insectary at Farnham Royal. It may almost be described as a nocturnal species, preferring the shade, and never building its orb-web in sunny situations. Blackwall[1] remarks that it is " more abundant in England and Wales than generally supposed to be, its apparent scarcity being attributable to its nocturnal habits and the care with which it conceals itself during the day ; preys chiefly on moths."

Pachygnatha degeerii, Sund.

This is a common species in Britain and on the Continent. It is fairly easy to recognise with its black cephalothorax and the black and white pattern on the abdomen. It proved to be a good *Smynthurus* predator. Spiders of the genus *Pachygnatha* do not build webs of any kind, although they belong to a family characterised by the orb-weaving habits of the majority of its members. Their habitat is on the ground under leaves, etc., particularly in damp or marshy situations.

Singa hamata, Clerck.

Experiments on this species were not carried to completion owing to the difficulty in obtaining sufficient food at the time of the year (beginning of December). In any case its value as a predator is somewhat doubtful. The genus includes small species with short legs, which live among low herbage in damp situations. Although not a very common species, Blackwall[1] remarks that *S. hamata* is " sometimes found in great abundance locally."

Evophrys sp. (immature).

This is the only member of the SALTICIDAE or " Jumping Spiders " represented in the Arachnid predators of *Smynthurus viridis*. These spiders do not construct a web but carefully stalk and spring upon their prey. The quadrangular cephalothorax, which supports the enormous eyes (necessary for their mode of living), renders the SALTICIDAE fairly easy to recognise.

This concludes the list of insect and spider predators tested in the laboratory ; however, it should be mentioned that this list represents but a small proportion of the total number of insects and Arachnids to which *Smynthurus* was fed, in the hope of discovering and putting to quantitative trial an efficient predator of the Collembolan. There now remains to be considered the general characteristics of the different groups of predators, the characters common to the most efficient predators, and finally to contrast and compare the insect and Arachnid groups, with a view to eliciting, if possible, further information which might reinforce existing knowledge as to the significance of the different species.

3. Comparison of Insect with Arachnid Predators.

In regard to the insect group of predators, it is obvious that the family STAPHYLINIDAE contains the greatest number of predators as well as a large majority of the more efficient ones, and thus collectively may be regarded as exerting a greater check upon the increase of the *Smynthurus* population in nature than any other single family of insects. Further, the two most efficient predators of the group

belong to the same subfamily (PAEDERINAE) and the same tribe (PAEDERINI). The next best Staphylinid predator is *Stenus cicindeloides*, belonging to the subfamily STENINAE. These are all small insects, but with a very distinctive appearance, so that it is impossible to mistake them, and although they present considerable diversity in some respects, yet in others they have much in common. For example, they are found in greatest number and variety in the temperate regions of the globe (but not exclusively so), prefer damp situations as a general rule, and are probably all carnivorous. These features all reinforce existing information as to the probability of *Smynthurus viridis* being a common item in the food supply of certain species of *Stenus*. Here it should be mentioned that Dr. Myers has found two other species of *Stenus* which are predatory upon *Smynthurus*, namely, *S. paganus* and *S. speculator*. By far the majority of the insect predators regarded as "good" or "fairly good" were taken during the months of September-October, May-June, and it is noteworthy that the *Smynthurus* population during either of these two-monthly periods is larger than in any other two consecutive monthly periods throughout the year, despite the fact that the insect population as a whole is highest during July-August.

As regards the spider group of predators, the family THOMISIDAE contains a greater number of efficient predators than any other family of spiders, and it is interesting to investigate why this should be so, although it must be borne in mind that the EPEIRIDAE and LINYPHIIDAE are not greatly inferior in this respect. The first and most obvious feature lies in the mode of obtaining the prey. *Smynthurus viridis* by no means affords an easy victim to predators, owing to its tremendous leaping power, which it exercises on the slightest provocation. THOMISIDAE, being spiders which do not build webs, either ambush their prey or chase and stalk it, pouncing when opportunity offers. They conceal themselves under fallen leaves, herbage, under stones, etc., and are widely distributed over the globe. On the other hand, the EPEIRIDAE and LINYPHIIDAE are web-spinners, of sedentary habit, seldom travelling far from the snare set for their victims. Coarse grass and other herbage seem to be the typical haunt of these families. Hence it happens that the best spider predators are typically ground-loving forms, making occasional excursions up the coarse stems of grass, but living generally within 6 inches of the ground stratum. This is what one would naturally expect, provided that the so-called efficient predators had been judiciously and carefully selected, because the six inches above ground-level represents the vertical range of activity of *Smynthurus*. The species in question are as follows:—three Thomisids, the Erigonid, *Lephthyphantes zimmermanni*, and *Pachygnatha degeerii* (the Epeirid with non-characteristic habits).

On account of the relatively small thorax and large rotund abdomen with a definite pattern, some of the Epeirids and Linyphiids above mentioned present a striking resemblance to an adult *Smynthurus viridis*, when viewed from the dorsal surface, but whether this has any significance or is purely an accident it is perhaps wiser not to hazard a definite opinion.

Coming to a comparison of the relative efficiency of the insects and spiders, we broach a difficult subject, which must be postponed for fuller consideration until after we have examined the effect of biotic factors upon the *Smynthurus* population in nature as derived from quantitative field data. However, judging from the preceding information obtained from laboratory experiments we may draw up a list of predators and place them in their order of efficiency. Taking into consideration only those regarded as good or fairly good predators, and using No. 2 Criterion of Efficiency, the list is as follows:

(1) *Forficula auricularia*, L.; (2) *Paederus littoralis*, Grav.; (3) *Coccinella septempunctata*, L.; (4) *Tibellus oblongus*, Wal.; (5) *Xysticus* sp.; (6) *Lephthyphantes zimmermannii*, Berth.; (7) *Philodromus* sp., *Erigone* sp., and *Cyrtosus cyanipennis*, Er.; (8) *Lathrobium brunnipes*, F.; (9) *Pachygnatha degeerii*, Sund., and

Meta segmentata, Clerck; (10) *Erophrys* sp., and *Philonthus laminatus*, Creutz.; (11) *Stenus cicindeloides*, Sch.; (12) *Philonthus politus*, F.

Although this list contains the majority of the most efficient predators of *Smynthurus viridis*, others doubtless exist, especially amongst the LINYPHIIDAE, STAPHYLINIDAE, and perhaps CARABIDAE. Nor does the list represent the order of utilisation for purposes of biological control, since it takes no account of ecological relationships between prey and predator, seasonal periodicity, numerical abundance, economic significance, or feasibility of collecting or rearing in adequate numbers. All these factors must receive critical analysis in making a judicious selection of predators. The final choice of predators, their significance in checking the increase of the *Smynthurus* population, and the feasibility of their economic utilisation, will be considered later in conjunction with the field data.

4. Effect of Density upon Rate of Population Increase.

There now falls to be considered, briefly and somewhat tentatively, the little known influence of one organism upon another of the same or a different species; in short, the effect of density upon rate of population increase. In order to obtain some idea of the action of this factor upon reproduction a series of experimental populations were set up, in which the only difference as regards environmental factors was space per individual. The experimental universes consisted of 7 glass jars of equal volume, in which the numbers of *Smynthurus* were placed in the following geometrical proportions:—2^1, 2^2, 2^3, 2^4, 2^5, 2^6, 2^7—it being deemed advisable to adopt this ratio in view of the fact that populations tend to increase in the form of a geometrical progression, provided that there are no inhibiting influences. The space available per individual, therefore, decreased in the ratio:—

$$\frac{1}{2^1}, \frac{1}{2^2}, \frac{1}{2^3}, \ldots\ldots\ldots\ldots\ldots \frac{1}{2^7}.$$

When all the individuals died off the number of eggs which had been deposited in each experimental container were counted. The experiment was repeated and the results of both experiments are presented below:—

Space per individual	$\frac{1}{2^1}$	$\frac{1}{2^2}$	$\frac{1}{2^3}$	$\frac{1}{2^4}$	$\frac{1}{2^5}$	$\frac{1}{2^6}$	$\frac{1}{2^7}$
No. of eggs (Experiment 1)	0	0	36	25	86	90	60
No. of eggs (Experiment 2)	0	0	0	8	320	465	440
No. of eggs per individual (Experiment 1)	0	0	4·5	1·5	2·7	1·4	0·47
No. of eggs per individual (Experiment 2)	0	0	0	0·5	10	7·3	3·4

Taking into consideration only the higher densities (since perhaps the lower ones do not include a sufficient number of individuals to eliminate the possibility of there being many more males than females) it is clear that the number of eggs per individual decreases approximately in the form of an arithmetical progression from 2^5 upwards. Now the density existing in the case of the container with 32 individuals amounted to one *Smynthurus* per 2 cc., a concentration which was not approached in the field (in this climate, where the population is well controlled) even when the *Smynthurus* population reached its maximum. However, if the effect obtained above is not specific and can be induced by the presence of other species or organisms, which is not likely, then it would come into operation very much sooner, probably before "plague" dimensions were attained. The manner in which the above effect operates is probably in part due to continual disturbance and interruption of females in their attempts to oviposit, and partly due to psychological influences. That *Smynthurus* is very sensitive to contact influences can be readily demonstrated by placing a large

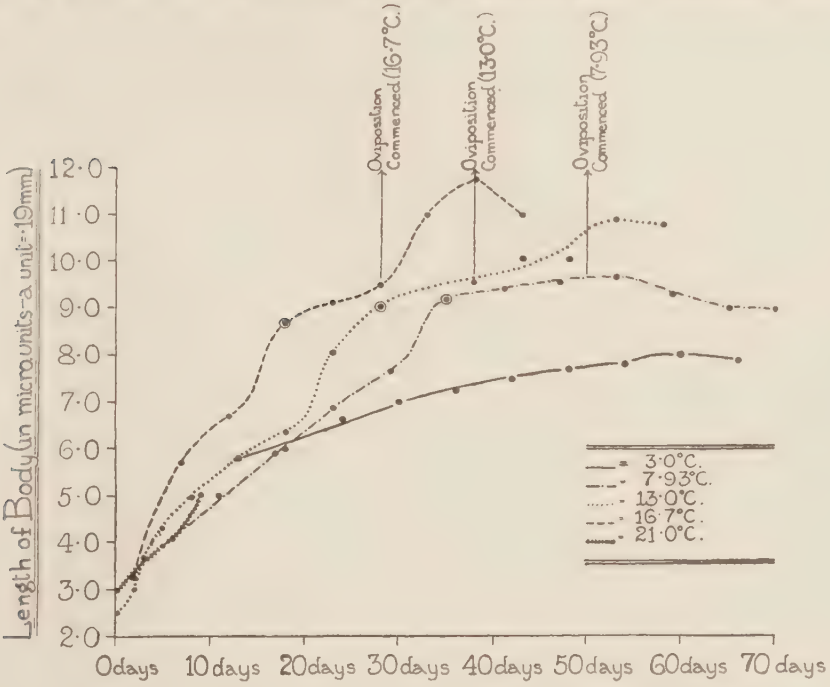
number inside a glass jar, when they will be seen to distribute themselves almost uniformly over the interior area, as a result of each individual attempting to avoid its neighbour.

This density factor has only been investigated in a very few instances, so that very little is known about it, and I only put forward the above remarks in a somewhat tentative fashion. If the example above holds good for other species it would appear that populations automatically check their own increase in virtue of the density effect, and that the organism itself imposes the ultimate limit to its own increase, although this effect would doubtless only come into operation when all other factors inhibiting population increase are at, or near, the optimum for the species.

V. Effect of Physical Environmental Factors.

1. Effect of Temperature upon Growth Rate and Total Growth.

It soon became evident after a few preliminary experiments with *Smynthurus* nymphs that slight differences in temperature produced very profound differences in their rate of growth and even total growth, while it was evident from the field data that the length of time required for the attainment of sexual maturity varied considerably in the successive generations, becoming gradually shorter as summer advanced



Graph 3. Effect of temperature upon growth of *Smynthurus* nymphs.

and gradually longer with the approach of winter. Accordingly, several experiments were carried out to determine the effect of different temperatures upon the growth of nymphs, and these are presented in Graph 3. The graph has been so constructed as to be almost self-explanatory, and the tracing out of the various curves should convey to the mind a more accurate representation of the facts than can be expressed in words. However, the following notes will facilitate its interpretation.

(i) With the exception of 21° C., the curves represent the absolute growth rate under conditions of slightly fluctuating temperatures, so that 16·7° C., 13·0° C., and 7·93° C., represent mean temperatures, as calculated from 6-hourly intervals on a continuous chart record. The temperatures of 21° C., and 25° C., are constant within ±0·5° C.

(ii) In order to convey some idea of the relationship of these temperatures to outdoor conditions, it may be stated that the curve for 7·93° C. was plotted from nymphs placed outside from 11th October to 20th December, the daily mean temperature from 15th May to 10th July (1929) at Farnham Royal (in a Stevenson screen) was 12·4° C., and the daily mean temperature from 11th July to 19th September (1929) was 16·4° C.

(iii) It will be observed that in the case of the 13·0° C. growth curve, the typical sigmoid form is very closely approximated, as has already been described (p. 109). However, the characteristic cycles in the *Smynthurus* growth curve are still distinctly indicated above and below 13·0° C., namely, at 16·7° C., and 7·93° C., respectively, although not to such a marked degree. This suggests that at temperatures significantly removed from 13·0° C., growth proceeds abnormally in this species, being over-accelerated or unduly retarded. The ultimate effects of the abnormal growth rate will be observed later, when we come to consider fecundity and longevity.

(iv) The higher the temperature (up to a certain limit) the more rapid is the growth rate—as one would expect ; also, the higher the temperature (up to a certain point) the greater is the total amount of growth—which one would not necessarily expect. The total growth, being the length of the body expressed as a percentage of the total at 16·7° C., is as follows :—

Temperature ...	16·7° C.	13·0° C.	7·93° C.	3·0° C.	21·0° C.	25·0° C.
Percentage ...	100	91·0	82·2	68·0	42·5	38·3

When the data in this table are plotted in the form of a curve, with percentages of total growth as ordinates and temperatures as abscissae, the points on the graph corresponding to the four lower temperatures are found to lie almost exactly on a straight line, indicating that total growth in *Smynthurus* is directly proportional to the temperature, up to 16·7° C., at which maximum growth occurs. Thereafter a sudden and very rapid falling off takes place up to 25° C., beyond which the nymphs (even under optimum humidity conditions) cannot exist for any length of time.

(v) The growth rate also increases up to 17·0° C. (approx.), and after a certain temperature (somewhere between 17·0° and 21·0° C.) is exceeded, decreases rapidly. Since growth continues, although very slowly, at 3·0° C., proceeding at a maximum pace about 17·0° C., and then rapidly falling off, it is evident that the range of activity of *Smynthurus*, even where humidity conditions are at an optimum (these experiments being carried out in an almost saturated atmosphere), is situated low down on the temperature scale in comparison with other insects.

(vi) An extremely interesting feature in this graph is indicated by the double circles and the arrows. The former indicate the period during growth at which 75 per cent. of the nymphs are in the seventh instar, sexual maturity being attained in this stadium. It will be observed how remarkably constant is the attainment of sexual maturity, with reference to the growth cycles, despite differences in temperature, this phase being located very definitely on the crest of the second growth wave. Further, the attainment of sexual maturity is always followed by a period of decreased growth rate, during which, presumably, food is directed towards accumulation of yolky material in the ova, indicating an antagonism between growth and

reproduction. These growth curves are dominated by the course of growth in the females, since the sex ratio is at the highest 25 : 100, when expressed as number of males per hundred females.

TABLE V.

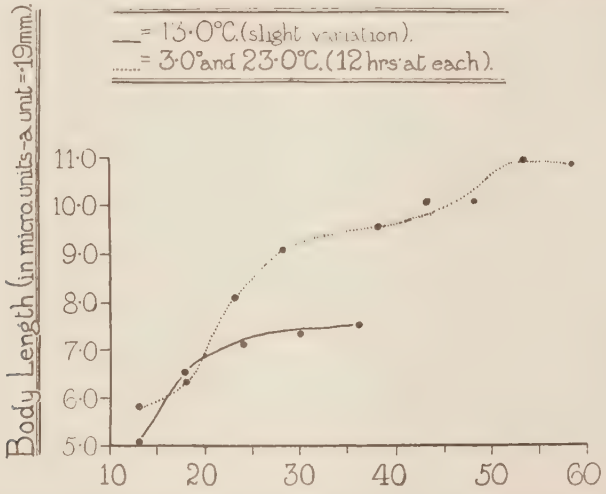
Temperature	Average length of *Smynthurus* nymphs throughout growth period (in micro. units.—1 m. unit = 0·19 mm.)												
3·0° C.	5·80	6·00	6·66	7·00	7·25	7·50	7·66	7·83	8·00	7·87	-	-	—
3·0° and 23·0° C. (12 hrs. at each) ...	5·05	6·50	7·11	7·50	—	—	—	—	—	—	—	—	—
Time (in days)... ...	13	5	6	6	6	6	6	6	6	6	-	—	—
7·83 C.	3·95	5·0	5·9	6·87	7·68	9·21	9·42	9·58	9·66	9·33	9·00	9·00	—
Time (in days)... ...	5	6	6	6	6	6	6	6	6	6	6	6	-
13·0 C	2·51	3·00	4·35	4·97	5·8	6·35	8·05	9·05	9·55	10·05	10·05	10·90	10·80
Time (in days)... ...	0	2	3	3	5	5	5	5	10	5	5	5	5
16·70° C.	3·25	5·68	6·71	8·75	9·1	9·5	11·0	11·75	11·0	—	—	—	—
Time (in days)	2	5	5	6	5	5	5	5	5	-	—	—	—
21·0° C.	3·00	3·70	4·08	5·00	—	—	—	—	—	—	—	—	—
25·0° C	3·00	3·88	4·00	4·50	—	—	—	—	—	—	—	—	—
Time (in days)... ...	0	3	3	3	—	—	—	—	—	—	—	—	—

(vii) It will also be observed that the higher the temperature (up to 17° C. approx.) the smaller the individuals and the shorter the time interval when sexual maturity is reached, the time required at 16·7° C., being almost exactly half that required at 7·9° C. At 21·0° C. and 3·0° C. the nymphs never attain to the seventh instar, dying off before this is reached on account of the very adverse temperature effects, such temperatures being too far removed from the normal growth temperature for *Smynthurus*. Again, it will be observed that oviposition of the first egg batch initiates the third and last growth cycle, but the latter does not appear in those nymphs reared at 7·9° C. This seems due to the fact that the nymphs gradually died off on account of a general reduction in metabolic vigour at this somewhat low temperature, so that adverse secondary factors, such as fungus and bacterial attacks, gained ascendancy, resulting in the death of the nymphs. The gradual falling off in body length at the close of the growth period is a definite characteristic of these insects, there being a general shrinkage in size just prior to, and during, the onset of conditions resulting in the death of the individual.

Graph 4 illustrates the effect of violent fluctuations in temperature upon the growth of *Smynthurus* nymphs. A batch of these (10 in all) was subjected to temperatures of 3·0° and 23·0° C., for 12 hours alternately, giving a mean temperature of 13·0° C. In comparison with the slightly fluctuating temperature of 13·0° C., it is apparent that these violent fluctuations have a marked initial stimulating effect, but eventually prove harmful, and result in a rapid decrease in growth rate. Thus varying temperatures stimulate growth, provided that the variation be not too violent.

2. Effect of Humidity upon Growth Rate and Total Growth.

Under natural conditions humidity tends to vary inversely with temperature; it was obviously desirable, therefore, to isolate the effects of temperature and humidity upon the several phases in the life-history of *Smynthurus*, in order to demonstrate how much of the effective action was attributable to the respective factors constituting the combined effect, as high temperatures and low humidity usually act simultaneously in nature, with the exception of certain tropical areas, in which *Smynthurus* cannot exist, as will be shown later. Previous experiments had shown that the successive stages in the life-history become decreasingly sensitive to the adverse effects of low humidities. Hence to demonstrate the effect of low humidities upon growth one

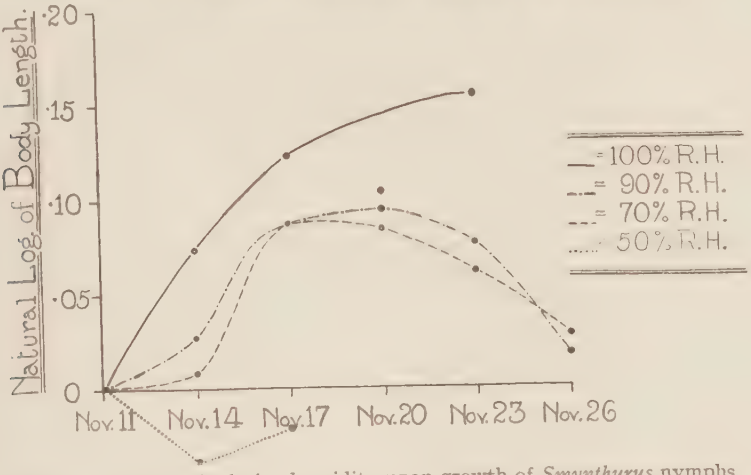


Graph 4. Effect of severe fluctuations in temperature upon growth of *Smynthurus* nymphs.*

had to effect a compromise between choosing an early nymphal stage, which would demonstrate growth but could not survive long at the low humidities, and a later stage which could resist the adverse effect of low humidity for a longer period but was incapable of any considerable amount of further growth. Eventually it was decided to use fifth and sixth instar nymphs, these being distributed equally in the respective humidities, namely, 50, 70, 90, and 100 per cent. R.H., using 10 individuals for each humidity and making measurements every third day. Each individual was subjected to three different measurements (as in all experiments involving the effect of environmental factors upon growth), (1) width of head capsule—in order to ascertain whether a moult had taken place or not, (2) width of abdomen, and (3) length of body from anterior end of the head to tip of the abdomen. Two experimental difficulties encountered should be mentioned: firstly, the fact that the individuals had to be removed from the experimental humidity chamber for a few moments in order to be measured; and secondly, the food was always supplied fresh and thus several hours elapsed before it came into humidity equilibrium with the experimental atmospheric humidity. It was deemed wiser, however, to do so rather than to supply food of the same moisture content as the atmosphere in the container, the former method being regarded as a closer approximation to natural conditions, since the plant can maintain its moisture content (if the humidity is not excessively low) by drawing upon the reserve of moisture in the deeper layers of the soil, the latter being unavailable to *Smynthurus*.

* The explanations of the curves have been accidentally reversed in the graph; the dotted line (not the solid) represents 13°C., and *vice versa*.

The growth curves of *Smynthurus* nymphs under the above-stated conditions are presented in Graph 5 (for data see Table VI), and an account of the experimental difficulties mentioned should perhaps be regarded as indications of the *relative* effect of the different humidities, rather than the *absolute* effect. The actual figures have been transformed into a percentage of the original size, and then converted into the



Graph 5. Effect of relative humidity upon growth of *Smynthurus* nymphs.

natural logarithm, the transformation having the effect of eliminating small fluctuations without obscuring the main features, which the curves are meant to demonstrate; and further, the natural logarithms of the successive growth measurements represent the average relative growth rates for each successive period, *i.e.*, the increase per unit of time per unit of growth attained.

TABLE VI.

Relative humidity	Average length of *Smynthurus* nymphs (in micro. units—a unit = 0·19 mm.)						
100 per cent. saturated ...	7·05	7·60	8·00	7·83?	8·25	—	Actual body length in micro.-units.
90 per cent. saturated ...	6·70	6·90	7·31	7·37	7·25	6·83	
70 per cent. saturated ...	6·80	6·85	7·44	7·35	7·25	7·00	
50 per cent. saturated ...	7·05	6·75	6·92	—	—	—	
100 per cent. saturated ...	100	107·8	113·5	110·0?	117·0	—	Same as above, reduced to percentage of original size.
90 per cent. saturated ...	100	103·0	109·1	110·0	108·2	102·0	
70 per cent. saturated ...	100	100·7	109·4	108·9	106·6	102·9	
50 per cent. saturated ...	100	96·0	98·2	—	—	—	
Time (in days)	0	3	3	3	3	3	

It will be observed that—

(i) One hundred per cent. relative humidity is decidedly the optimum, resulting in both greater growth rate and maximum growth. While the difference in growth rate and maximum growth between 70 per cent. R.H. and 90 per cent. R.H. must

be regarded as almost insignificant, the difference produced by 100 per cent. as compared with 90 per cent. is considerable. This is apparently due to the fact that although a decreasingly low relative humidity increases the rate of loss of moisture, *Smynthurus* can only counteract this loss when access to liquid moisture, either via the food or a liquid film, is available. In the lower humidities, therefore, the only source of moisture is the food, while in the 100 per cent. R.H. both food and environment act as sources of supply, the slightest variation in temperature producing condensation of liquid moisture in the saturated atmosphere.

(ii) In those individuals subjected to 50 per cent. R.H. there actually takes place a considerable decrease in size during the first three days, followed by a definite recovery during the next three days, the recovery, however, never being complete. It should be noted that this recovery is not due to the elimination by death of a certain number of individuals less tolerant to adverse humidity conditions than their fellows, and thereby raising the average size of the remainder, but is an actual increase in size of the individuals, resulting undoubtedly from a certain degree of acclimation. (One does not require to experiment long with *Smynthurus* to realise the capacity for acclimation, and varying degrees of tolerance to adverse circumstances, exhibited by these primitive insects, even by individuals hitherto subjected to identical conditions—this physiological variation rendering laboratory work a very dangerous source from which to attempt broad generalisations, when unaccompanied by field data.)

(iii) The gradual reduction in size after attaining their maximum, in the 70 per cent. and 90 per cent. saturated atmospheres, can be explained as the result of a gradual reduction in vitality in the struggle against adverse circumstances, so that the resistance is gradually lowered, and the individual eventually succumbs.

(iv) If the growth curves be plotted from the width of the abdomen, instead of body length, similar results are obtained, but the differences tend to be exaggerated on account of the collapsible nature of the abdomen in *Smynthurus*, so that more reliable results accrue by using body length as a growth criterion.

(v) By examining the data on the width of the head-capsule during the period at which maximum growth is attained in the respective humidities it is found that there is not a great divergence in the four humidities as to the instar reached, despite the difference in growth, showing that the latter factor is not the only one determining whether a moult will or will not take place.

3. Effect of Soil pH Value upon Growth Rate and Total Growth.

Very few laboratory studies in regard to the rôle of hydrogen ion concentration in insect development have been undertaken, despite the known importance of hydrogen and hydroxyl ions in catalysing many biochemical reactions, especially those involving enzymes. Because of the neglect of this important phase of investigation we know very little concerning the rôle of these ions in such a common and universal phenomenon as insect metamorphosis, although a valuable beginning has been made by Fink[6] who has shown that (i) the reaction of the body fluids of insect species is different in species belonging to different orders, and that (ii) in *Leptinotarsa decemlineata*, Say, at least, there are marked changes in pH value throughout the course of development from egg to adult. The relation of soil pH value to insect distribution has received more appreciation, although by no means the attention it merits, and this will be briefly referred to when we proceed to consider the relation of soil type to the geographical distribution of *Smynthurus*.

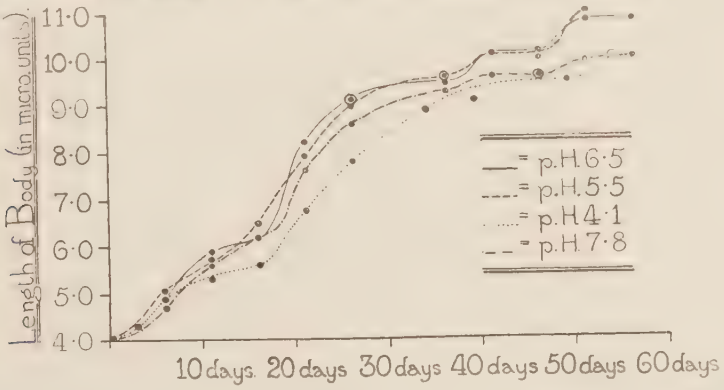
In order to determine whether soil reaction would produce a differential effect upon the growth of *Smynthurus* nymphs, an experiment was conducted in which 40 early-instar nymphs were reared to maturity on soils of different types (each nymph being isolated in a small glass vial) and utilising ten for each of the four soils.

Fresh food and soil was supplied as required about every fifth day, the soil being kept continually moist with distilled water, and the food consisting of white clover leaves. The soils employed in this experiment were natural soils, it being deemed inadvisable to alter the hydrogen ion concentration artificially, since a considerable interval of time must elapse before the various reactions involved in such a procedure would resume their normal equilibrium. Soils extending over a sufficiently wide range on the pH notation were obtained whilst on vacation in Scotland, and the pH value determined by the potentiometer method in order to check the values with my own colorimetric standards.

TABLE VII.

Soil pH value	Average body length of *Smynthurus* reared on soils of different pH value												Time for attainment of 7th instar	Deviation from optimum pH (6·3)
	Length in micro. units												Days	
pH 4·1 ...	4·0	4·3	4·9	5·3	5·6	6·75	7·8	8·9	9·1	9·6	9·5	10·0	56	2·2
pH 5·5 ...	4·0	4·35	5·05	5·70	6·50	7·90	9·00	9·60	10·1	10·0	11·0	—	36	0·8
pH 6·5 ...	4·0	4·35	4·90	5·90	6·20	8·20	9·10	9·50	10·1	10·1	10·8	10·8	26	0·2
pH 7·8 ...	4·0	4·25	4·70	5·60	6·20	7·60	8·60	9·30	9·60	9·60	9·90	10·0	46	1·5
Time (in days)	0	3	3	5	5	5	5	10	5	5	5	5	—	—

The four different soils in the experiment had the respective pH values of 4·1, 5·5, 6·5, and 7·8. The first and last types are somewhat uncommon, although soils more acid than 4·1 and more alkaline than 7·8 are by no means unknown. The majority of agricultural soils, however, have a value ranging somewhere between 5·0 and 7·0 on the pH scale. In view of the economic relationship of *Smynthurus*



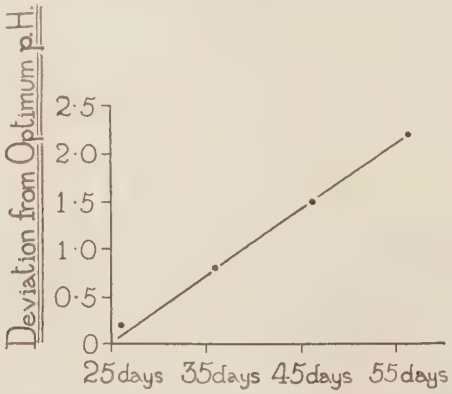
Graph 6. Effect of soil pH value upon growth of *Smynthurus* nymphs.

to the production of leguminous crops it may be mentioned here that lucerne is very intolerant of acid conditions, preferring a slightly alkaline soil, *i.e.*, over pH 7·0, and that clovers also grow best under slightly alkaline conditions, but exhibit a greater degree of tolerance to acid conditions than lucerne. The results of the experiment have been presented graphically (see Graph 6), the chief points of interest being as follows :—

(i) The experiment clearly demonstrates that soil pH value produces a differential effect upon growth of *Smynthurus* nymphs. Although there is not a great deal of difference in the growth curves of the nymphs reared on soils of pH 5·5 and 6·5, respectively, yet from the fact that the growth curve for pH 6·5 more closely approximates the normal growth curve for *Smynthurus*, and from other considerations in relation to sexual maturity and fecundity, the optimum soil pH value in these experiments is undoubtedly 6·5. Actually, the optimum pH would appear to lie somewhere between 5·5 and 6·5, and much nearer to the latter than to the former.

(ii) The differential effect upon growth produced by soils of pH 7·8 and 4·1 is quite considerable, being a decrease from the optimum of 8·4 per cent. and 21·1 per cent., respectively, when growth is practically complete, while the effect upon fecundity and time required for the attainment of sexual maturity is greatly intensified. The double circles on the respective growth curves indicate, as before, when 75 per cent. of the nymphs have reached the seventh instar, the stadium in which sexual maturity is attained. It will be observed that the time required to reach this stage on soil of pH 4·1 is slightly more than double that required on soil of pH 6·5, and the time required on soil of pH 7·8 is slightly over 150 per cent. of that required on the optimum soil.

(iii) Now if the degree of departure from the optimum pH (taking this to be 6·3, since these experiments suggested that the actual optimum lay slightly on the acid side of 6·5) be plotted against the time required for the attainment of sexual maturity by 75 per cent. of the nymphs, then it is found that those two variables have a linear relationship, *i.e.*, the time required for sexual maturity is a linear function of the deviation from optimum soil reaction, when expressed in terms of the pH notation. This has been presented diagrammatically in Graph 7, and although only four points on the pH scale have been considered, their approximation to a straight line is so close that the above linear relationship can hardly be doubted.



Graph 7. Time of attainment of 7th instar.

(iv) The characteristic physiological rhythm underlying the growth process in *Smynthurus* is again clearly demonstrated by these curves of growth on different soil types, the maximum growth rate again being shown in the second cycle. The three recurrent cycles are convincingly demonstrated and also the analogous effect of low temperature and a deviation from optimum pH, in that both produce a slowing up in the growth rate, a retardation in the time of attainment of sexual maturity and an increase in size when the latter stage is reached. This slowing up of the growth rate, as in the case of low temperatures, results in a lateral displacement of the respective growth curves to the right.

(v) The mode of action by which soil pH value brings about its effect upon the growth process in *Smynthurus* is not altogether easy of interpretation, but would appear to be associated with the question of ionic balance, adverse effects resulting from a disharmony between the ionic equilibrium obtaining in the insect's body fluids and the soil complex, the latter being an important feature of the diet.

4. Effect of Various Combinations of Temperature and Humidity on Fecundity.

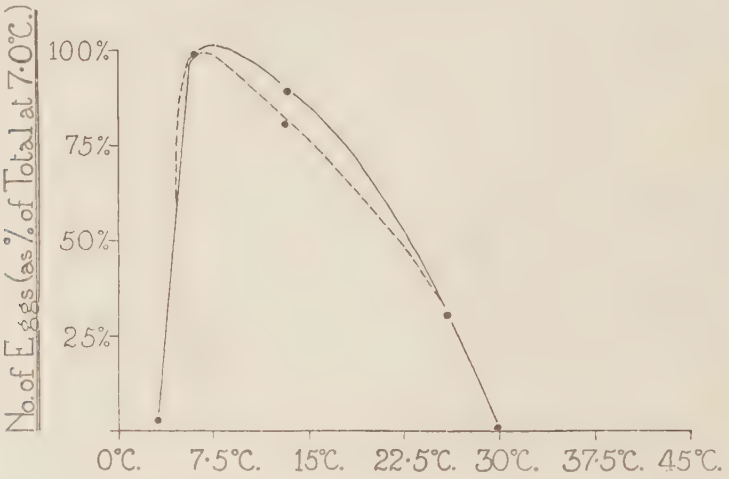
This environmental effect was determined by a series of experiments in which the adults were taken direct from the field, supplied with abundance of clover leaves for food as well as soil of optimum pH value, and subjected in each experiment (using 10 individuals in each) to a different combination of temperature with humidity, making use of 25 different combinations. Each experiment was allowed to run for a week, enough food being added at the beginning to supply the requirements for that period, so that the difficulty of having to open the humidity chamber was thereby avoided. At the end of a week's time each experiment was examined and the number of eggs deposited was counted. The results of the experiments are shown in Table VIII, where there are presented (i) the actual number of eggs laid, (ii) the same calculated as a percentage of the maximum (which was obtained

TABLE VIII.

30° C.	0	0	4	7	0	No. of eggs
	0	0	1·8	3·2	0	Percentage of maximum
	14·4	11·2	7·3	3·7	0	Saturation deficiency
25° C.	0	40	70	72	68	No. of eggs
	0	18·2	31·8	32·7	30·9	Percentage of maximum
	10·7	8·1	5·3	2·7	0	Saturation deficiency
12·6° C.	0	136	195	175	131	No. of eggs
	0	61·8	88·6	79·5	59·5	Percentage of maximum
	4·3	3·2	2·2	1·1	0	Saturation deficiency
7·0° C.	0	168	220	200	198	No. of eggs
	0	76·4	100	90·9	90	Percentage of maximum
	3·0	2·2	1·5	0·8	0	Saturation deficiency
3·0° C.	0	0	8	x	24	No. of eggs
	0	0	3·6	x	10·9	Percentage of maximum
	2·4	·18	1·2	0·6	0	Saturation deficiency
	60% R.H.	70% R.H.	80% R.H.	90 % R.H.	100% R.H.	

at 7·0° C., and 80 per cent. R.H.), (iii) the saturation deficiency at each of the 25 temperature-humidity combinations. Several interesting points are brought out by

these figures, the most important of which are presented in Graphs 8, 9, and 10 as follows :—



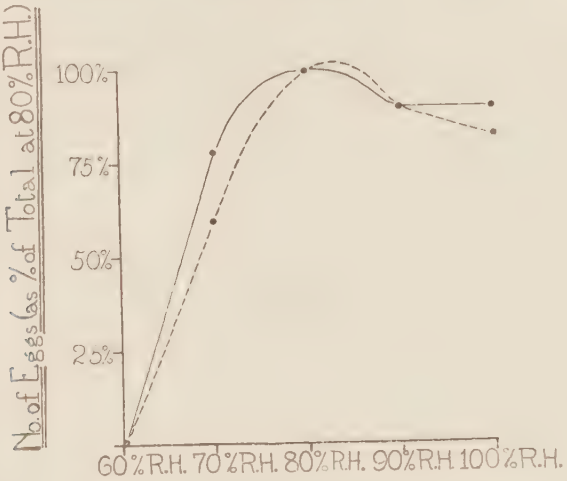
Graph 8. Effect of temperature upon reproduction.

(i) Both temperature and humidity have evidently a profound effect on the physiological process of reproduction and therefore on the potential number of individuals. As regards temperature, perhaps the most striking fact is the very low optimum, the latter not being far from that at which reproduction ceases, and much below the temperature optimum for growth rate and maximum growth.

(ii) In Graph 8, the effect of temperature at 80 per cent. R.H. (the optimum from these figures, although actually it probably lies between 80 and 90 per cent. has been plotted, and is indicated by the curve of the solid line, from which it will be observed that the rate of reproduction gradually rises from 30° C. (at which it is practically nil) with decreasing temperature, passing through an optimum slightly above 7° C., and then falling off very rapidly to 3·0° C., at which reproduction is again practically nil. In order to ascertain the effects of temperature under a variety of humidity conditions the columns in Table VIII have been summed horizontally, and the results presented by means of the broken line, from which it is evident that the effects in both cases are very similar. As the latter is based on 50 individuals instead of 10, the dotted curve probably gives a more accurate representation of the effect of temperature upon the reproductive processes of *Smynthurus*.

(iii) Graph 9 presents the effect of humidity on the rate of reproduction, the solid line indicating the effect of humidity at the temperature corresponding to the temperature-humidity optimum for reproduction in *Smynthurus*, namely, 7·0° C. The dotted line indicates the effect of humidity under a variety of temperature conditions, as obtained by summing the columns in Table VIII vertically. The two curves are again fairly similar, but the latter, for the same reasons as stated in connection with the temperature effect, is probably a more accurate indication of the effect of humidity upon rate of reproduction. Graph 9 clearly demonstrates the very limited range of humidity conditions in which normal reproduction is possible, the reduction in the number of eggs deposited falling off very rapidly as the humidity falls from 80 per cent. to 70 per cent. At the latter degree of saturation, reproduction is only 75 per cent. of that under optimum humidity conditions, falling off at an increased rate to nil at 60 per cent. R.H.

(iv) In looking over Table VIII, the interesting point arose as to the relative proportions in which the constituent factors of a temperature-humidity effect might become influenced as one proceeded in a direction away from that particular combination productive of the maximum response in reproduction. Since saturation deficiency combines temperature and humidity in a single unit, being a function of both, it can be utilised as an index of the change in response to changes in any one variable, when the other variable is kept constant. Hence Graph 10 illustrates the differences in rate of response to similar changes of temperature under different conditions of constant humidity. The graph clearly demonstrates that if temperature



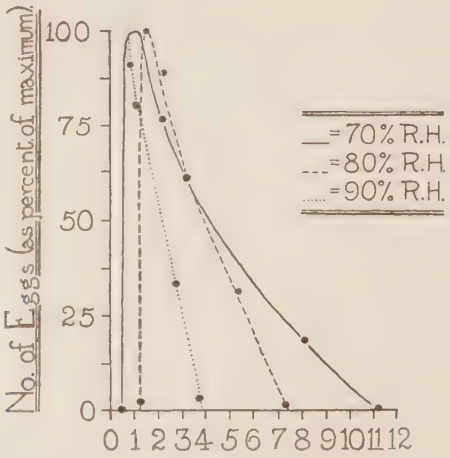
Graph 9. Effect of humidity upon reproduction.

be altered in either direction away from the optimum, the rate at which unfavourable temperatures can exert their adverse effect on the reproductive process of *Smynthurus* decreases as the departure from saturation increases, irrespective of the humidity optimum, or in other words, there is a differential rate of response to temperature with different conditions of humidity, becoming greater as the humidity conditions approach saturation, and reaching a maximum when the saturation deficiency is nil. This probably holds good for most, if not all, physiological processes, and the writer believes that a similar phenomenon in relation to dilution and rate of enzyme reaction has been proved. Hence to demonstrate the rate of response to temperature, a saturated atmosphere would appear to be the optimum, since under any other conditions of humidity, the saturation deficiency acts in a limiting capacity, with which temperature is indissolubly associated, the vapour pressure of water being a function of temperature.

(v) From the data in Table VIII it can also be shown that there is a differential rate of response to humidity with different conditions of temperature, being a maximum at the temperature corresponding to the temperature-humidity optimum. This would also appear to hold good for other vital processes as well as reproduction in *Smynthurus*. It is also evident that any attempt to utilise saturation deficiency as an index of the combined temperature-humidity effect must be restricted to constant conditions of relative humidity, since the response to changes in temperature becomes a different function of the latter with different relative humidities.

(vi) The results as a whole illustrate the very restricted temperature-humidity range under which anything approaching to normal reproduction can take place, so

much so, that even in Britain, where the conditions are climatically favourable to *Smynthurus* in comparison with many other geographical areas, the maximum rate of reproduction can only be obtained during a very limited period of the year, namely, April and October.



Graph 10. Saturation deficiency (in mm.).

5. Effect of Soil pH Value upon Fecundity.

Continuing the analysis of various environmental effects upon the life processes of *Smynthurus*, there remains to be considered the influence of soil type upon reproduction. An ever-increasing number of instances are being recorded in which soil type has an important bearing upon intensity of infestation in connection with insect pests. The effect may be purely a physical one depending upon the water-holding capacity of the soil, as determined by its texture and structure; on the other hand, there are undoubtedly influences of a chemical nature in soil, which determine its favourability or otherwise for a particular species. For instance, the factors influencing the choice by gravid females of particular sites for purposes of oviposition are often extremely obscure, but nevertheless of great determining significance. Indeed, it would appear that the faculties involved in the placing of the egg are very highly developed in their sensitivity to environment, although it is not always easy to locate the particular factor, or combination of factors, to which the organism responds. In regard to chemical conditions in the soil complex perhaps the most useful all-round general index is the hydrogen ion concentration, since it expresses in one unit a greater amount of information than any other index of soil type, with the doubtful exception of exchangeable base content, and the latter involves a somewhat laborious process for determination.

With the object of determining in quantitative terms this influence of soil upon the reproductive process in *Smynthurus*, an experiment was undertaken in which early instar nymphs were reared to maturity on soils of different pH value, and maintained there till death (to determine the effect on longevity). Since the same experiment was employed to ascertain the effect of soil upon growth, and this was previously reported, it will be unnecessary to repeat the details. The results of the experiment are as follows:—

(i) Soil type does not only influence appreciably the period over which oviposition takes place, by lengthening or shortening the normal reproductive phase in the life-

cycle of *Smynthurus*, but its effect upon the total number of eggs deposited is profound. The former effect is brought about as a result of the influence upon the time of attainment of sexual maturity, but is outstripped in significance by the latter.

(ii) The number of eggs deposited on the four different soils is presented in tabular form below :—

Soil pH value	4·1	5·5	6·5	7·8
Total no. of eggs ...	116	137	360	219
Percentage of maximum	32·2	38·1	100·0	60·8

From these results it is clear that the optimum pH value for reproduction is 6·5, or perhaps slightly on the acid side of this figure, and it will be recalled that this was also the optimum for growth. Any significant departure from 6·5 produces a great reduction in the number of eggs deposited, the detrimental effect of a soil on the acid side of the optimum being greater than one with a pH value equally removed from the optimum in the alkaline direction. An interesting fact in connection with the above is that the soils in Southern Australia, where *Smynthurus* is very abundant, have a pH value ranging between 6·0 and 7·0, *i.e.*, the optimum for *Smynthurus*, and hence contributing in a considerable degree, doubtless, to the intensity of infestation. The relative significance of climate, soil type, and other factors in determining the seasonal and geographical distribution of *Smynthurus* will be discussed in detail in a subsequent part.

(iii) The mode of operation by which soil brings about its effect upon the physiological processes of reproduction in *Smynthurus* is not fully comprehended, but would appear to be through its effect upon the nutrition of the adult, since soil forms an important part of the diet, *especially during the reproductive phase*. Briefly stated, pH value may be of little significance in itself, but what it may and would appear to do is to act as an index of the balance of ions in the soil complex, so that at the optimum pH the relative proportion of the various ions is such that they most closely approximate a state of equilibrium with the physiological conditions obtaining in the insect's body fluids. After all it is only reasonable to conclude that large quantities of acid or alkaline soil (*i.e.*, relative to the normal pH of the insect's digestive tract) passing through the intestine would result in a perturbation of the physico-chemical equilibrium of the cells lining the tract, and hence produce an adverse effect on metabolism and eventually affect the general well-being of the individual.

6. Effect of Soil Type upon Choice of Site for Oviposition.

One further experiment in connection with soil reaction remains to be considered, of which the object was to determine whether *Smynthurus*, if given the opportunity, could select certain types of soil for purposes of oviposition. With this object in view, four soils of pH 4·1, 5·5, 6·5, and 7·8, respectively (the same four as above), were placed in small uniform patches upon damp filter-paper in a glass container, and about 50 *Smynthurus* added, being supplied with clover leaves for food. At the end of three days the number of eggs which had been deposited on the respective soils was totalled and found to be as follows :—

pH 4·1—11 ; pH 5·5—39 ; pH 6·5—136 ; pH 7·8—11.

The experiment was repeated, using the same four soils as above, and so arranged that each soil occupied the quadrant of a circle. The eggs were removed and counted each day this time, the total result for the three days being as follows :—

pH 4·1—40 ; pH 5·5—66 ; pH 6·5—78 ; pH 7·8—24.

The results of these two experiments, taken together or singly, seemed so suggestive that it was determined to undertake a third experiment in order to obtain convincing proof of their significance. The same conditions were observed as previously, with the exception that the eggs were allowed to remain for four days, when they were removed and counted as before, with the following results :—

pH 4·1—38 ; pH 5·5—48 ; pH 6·5—80 ; pH 7·8—48.

The results of all three experiments are presented in tabular form herewith :—

Soil pH value	4·1	5·5	6·5	7·8
Experiment No. 1 ...	11	39	136	11
Experiment No. 2 ...	40	66	78	24
Experiment No. 3 ...	38	48	80	48
Total No. of eggs ...	89	153	294	83
No. of eggs as per cent.	14·4	24·7	47·5	13·4
Preference (very approx.)	1	2	4	1

Out of a total of 619 eggs, therefore, 47·5 per cent. were laid upon the soil of pH 6·5, 24·7 per cent. on the soil of pH 5·5, and 13·4 per cent. and 14·4 per cent. on soils of pH 7·8 and 4·1 respectively. The difference between the last two cannot be regarded as significant, and they thus rank as equally undesirable for oviposition purposes. In round numbers, soil of pH 5·5 is twice as attractive for oviposition as soil of pH 4·1 or 7·8, and soil of pH 6·5 is four times as attractive as the latter types. The above experiment again emphasises the significance of soil type in relation to numbers of individuals, and serves to reinforce the conclusions previously arrived at, as a result of the experiments in which *Smynthurus* was reared on a particular soil type, and thus could not exert a preference.

The experiment demonstrates conclusively that (i) *Smynthurus* can and does exhibit a selective action in the choice of soil for purposes of oviposition ; (ii) the particular sense which renders the insect capable of this discrimination is very likely taste ; (iii) pH may not be the ultimate determining factor, although it may be acting as an index of certain factors, or combination of factors, which render the soil complex physiologically desirable for the oviposition process, each egg being coated with an exudate of soil passed via the anus.

7. Effect of Temperature on Longevity.

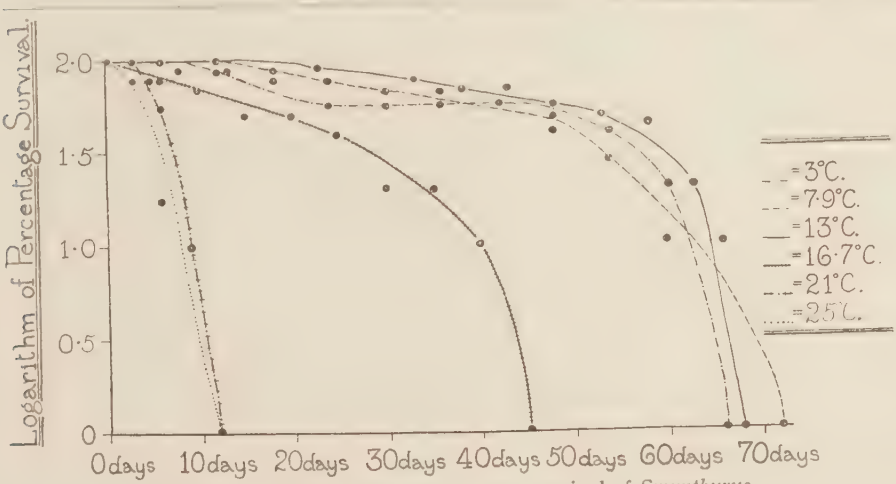
The rapid response of the growth and reproductive processes of *Smynthurus* to relatively slight environmental changes has now been demonstrated, and there still remains to be considered the influence of environment upon longevity. The effect of temperature under natural conditions is very evident from an examination of the field data, which seemed to indicate, in an empirical way, that with increasing temperature there was a gradual shortening of the total life-span.

This effect is presented quantitatively in Graph 11, in which the survival curves have been plotted for the same temperatures and the same individuals as those employed to demonstrate the effect of temperature upon growth, so that by referring to Graph 3 the relation between growth and survival at different temperatures can be considered. The percentage number of survivors is converted to a common logarithm and plotted

against age, equal gradients on such "survival curves" representing equal death rates.

TABLE IX.

Temperature	Percentage survival of nymphs throughout total life-span													
3·0° C.	100	100	90	80	60	60	60	60	40	40	20	0	—	—
3·0° C and 23·0° C. (12 hrs. at each)	100	90	90	50	10	0	—	—	—	—	—	—	—	—
Time (in days)	0	6	6	6	6	6	6	6	6	6	6	6	—	—
7·93° C.	100	100	100	80	80	70	70	60	60	30	10	10	0	—
Time (in days)	0	6	6	6	6	6	6	6	6	6	6	6	6	—
13·0° C.	100	100	90	90	90	90	80	70	70	50	50	40	20	0
Time (in days)	0	3	5	5	5	5	10	5	5	5	5	5	5	5
16·7° C.	100	80	70	50	50	40	20	20	10	0	—	—	—	—
Time (in days)	0	5	5	6	5	5	5	5	5	5	—	—	—	—
21·0° C.	100	100	60	10	0	—	—	—	—	—	—	—	—	—
25·0° C.	100	90	20	10	0	—	—	—	—	—	—	—	—	—
Time (in days)	0	3	3	3	3	—	—	—	—	—	—	—	—	—



Graph 11. Effect of temperature upon survival of *Smynthurus*.

The main features illustrated by Graph 11 are :—

(i) Temperatures over 13° C. cause a rapid rise in the death rate of *Smynthurus*, an increase in temperature of 4° C. (from 13° to 17° C.) reducing the normal life-span by 34 per cent., and an increase from 17° C. to 21° C., causing a similar reduction.

(ii) Temperatures below 13° C. cause a slight increase in the total life-span, provided that the temperature does not fall below 3° C. (approx.), when secondary effects come into operation on account of severe depression of metabolism, resulting in general lowering of vitality with decreased resistance to disease, to which the individual eventually succumbs.

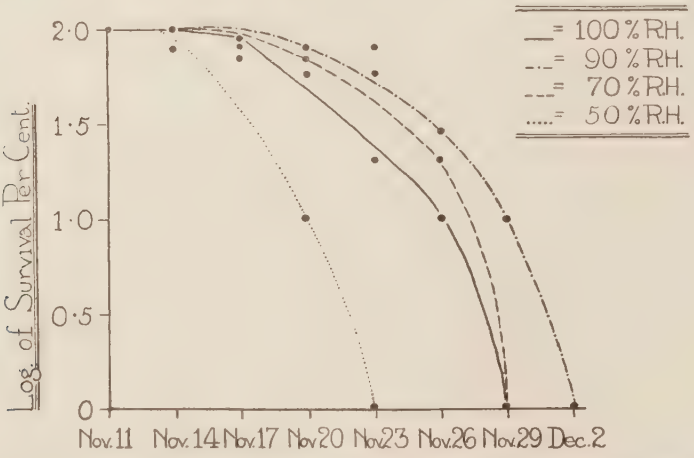
(iii) The optimum temperature for survival would appear to be 8° C. (approx.)—the temperature which depresses metabolism to a minimum without decreasing general vitality, and thereby inducing adverse secondary effects. It will be remembered that this was just about the optimum for reproduction, and also that it is only about 3·0° C. above the development zero of the egg stage. Further, experiments have shown that in a saturated atmosphere there is 100 per cent. mortality in 75 hours (approx.) at 30° C., in 12 hours (approx.) at 35° C., and in 3·5 hours at 40° C.

Table X.

Relative humidity	Common logarithms of percentage survival								
50 per cent. R.H.	2·0	1·9031	1·8451	1·0000	0	—	—	—	The time interval is 3 days
70 per cent. R.H.	2·0	2·0	1·9542	1·8451	1·7782	1·3010	0	—	
90 per cent. R.H.	2·0	2·0	1·9031	1·9031	1·9031	1·4771	1·0	0	
100 per cent. R.H.	2·0	2·0	1·8451	1·7782	1·3010	1·0000	0	—	

8. Effect of Humidity on Longevity.

It is evident from Graph 12 and numerous other experiments conducted by the writer, that 100 per cent. R.H. is the optimum for the survival provided that secondary effects do not enter, as they tend to do when *Smynthurus* (especially the nymphal



Graph 12. Effect of relative humidity upon survival of *Smynthurus* nymphs.

stages) is maintained continually in a saturated atmosphere. This effect is clearly brought out in Graph 12 where, although maximum growth took place in the saturated atmosphere, the nymphs lived slightly longer in the 70 per cent., and considerably longer in the 90 per cent. saturated atmosphere. The adverse effects of a continually saturated atmosphere are therefore secondary, the nymphs especially assuming a distended appearance, and 100 per cent. R.H. remains the optimum, provided that other conditions, such as food, temperature, etc., are conducive to maximum vitality and resistance to disease. This is confirmed by further experiments which have shown that the higher the relative humidity the greater the resistance of *Smynthurus*

to the adverse effects of high temperatures, *e.g.*, at 30° C. there is 100 per cent. mortality in 4 hours (approx.) at 0 per cent. R.H., in 6 hours (approx.) at 20 per cent., in 7 hours (approx.) at 40 per cent., in 51 hours (approx.) at 80 per cent., and in 75 hours (approx.) at 100 per cent. R.H.

9. Effect of Soil pH Value upon Longevity.

As previously mentioned, the effect of soil pH value would appear to be a nutritional one, so that marked departures from the optimum have the effect of reducing the speed of metabolism (as seen in the retarding effect upon growth) and thereby prolonging the total life-span. The difference, however, is not very marked and cannot be regarded as one of any practical significance.

VI. Inter-relationship of different Phases of the Life-cycle.

Having now considered the effect of various environmental factors upon the three vital processes, growth, reproduction, and longevity, there still remains to be briefly treated the relationship of these phases in the life-cycle of *Smynthurus* to each other.

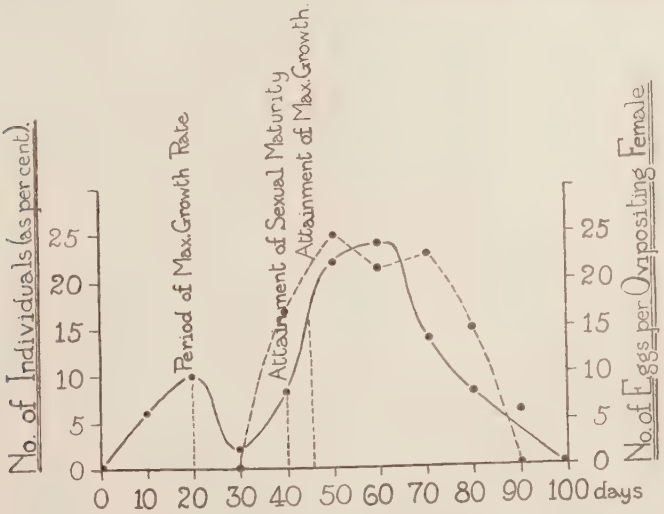
Table XI.

(i) Distribution of death rate with age (No. of individuals as per cent. of the original population).

(ii) Distribution of oviposition rate with age (No. of eggs per ovipositing female).

(i)	0	6	10	2	8	22	24	14	8	6	The time interval is 10 days
(ii)	0	0	0	0	16·75	25·3	21·3	22·8	15·2	0	

This is presented in Graph 13 (based on 50 individuals). The solid black line indicates the distribution of death-rate with age, at intervals of 10 days, and the broken line indicates the distribution of reproduction and the position of the reproductive phase, in relation to the total life-span. The scale for the solid line is on the left-hand side



Graph 13. Frequency curve to illustrate distribution of death rate.

of the graph, and that for the broken line on the right. The frequency curve for death-rate with age is bimodal, the first mode coinciding with the period of greatest growth, when 10 per cent. of the nymphs die off. Evidently the rapid growth phase has the effect of eliminating most of the individuals with an inherited constitutional defect or those which are physiologically unstable, since at this period metabolism is proceeding at a maximum pace and is most liable to aberration or injury. The second mode occurs about the 50—60 day interval (depending on the environment) when approximately 46 per cent. of the original population succumb, and it will be observed that the coincidence of this second mode with the maximum rate of reproduction is very close. Sexual maturity is attained during the last nymphal instar, *i.e.*, before the adult stage is reached, while the reproductive phase extends over approximately 50 per cent. of the total life-span.

VII. General Survey of Environmental Effects upon *Smynthurus*.

These experiments constitute the quantitative basis of the main arguments to be subsequently put forward to account for the natural control of *Smynthurus viridis*. Looking back over the results of these experiments as a whole, perhaps the most striking conception derived is the tremendous impress of environment upon population, operating through the actual and potential numbers of individuals. Secondly, one gains the impression of the individual as consisting of a heterogeneous assemblage of diverse physiological processes, each with its own optimum, rather than as a single harmonious physiological unit. Evidently, an organism with a physiological "make-up" like that of *Smynthurus*, having different optima for growth, reproduction, and the development of the egg, is endowed with a serious handicap from the start in the race for increase in numbers, and doubtless this is the case with most other organisms. Hence the optimum environment is one which presents the most effective compromise between a variety of conflicting physiological requirements on the part of the organism concerned. Thirdly, one is inclined to ask the question, to what extent does the so-called adaptation of the organism to its environment exist in actual fact? Doubtless evolution could not have taken place without adaptation, but it seems that the former has not proceeded to the extent often imagined, and fortunately so for the human race. The actual facts appear to be that population increase in a natural environment is seriously handicapped on account of the diverse physiological ensemble of the individual, and the fact that organisms flourish to the extent they do, is not due so much to their adaptation to the environment as to their increase in spite of it, on account of the enormous reproductive potential with which every creature is endowed.

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AN ECOLOGICAL STUDY OF THE "LUCERNE FLEA" (*SMYNTHURUS VIRIDIS*, LINN.)—II.

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Research Scholar of the Ministry of Agriculture and Department of Agriculture for Scotland.

Contents

		Page
I.	Seasonal variation in abundance of *Smynthurus*	152
1.	Guiding principles in selection of area for population census ...	152
2.	Method adopted in making the census of insect population ...	152
3.	Recording of fluctuations of environmental factors	153
4.	Seasonal variations of *Smynthurus* population in Field B. ...	153
5.	Developmental zero and the concept of temperature summation	154
6.	Temperature and rainfall as limiting factors to population increase	157
7.	Criteria of significant factors in analysis of environment	159
8.	Effect of rainfall upon oviposition	161
9.	Effect of rainfall upon development and emergence of nymphs ...	162
10.	Effect of temperature upon development and emergence of nymphs	162
11.	Effect of temperature upon survival of early instar nymphs and adults	165
12.	The timing of events in the life-cycle	167
II.	Geographical variation in abundance of *Smynthurus*	168
1.	Significance of soil reaction in the distribution of terrestrial animals	168
2.	Relation between the *Smynthurus* population and the soil reaction (pH value)	170
3.	Relation between the *Smynthurus* population and the yield of herbage	172
4.	Relation between the *Smynthurus* population and the percentage of Leguminosae in the herbage	173
5.	Influence of biotic factors upon the *Smynthurus* population ...	173
6.	Relative significance of factors in the controlling complex in the south of England	175
7.	Prediction of complete geographical range of existence	176
8.	Prediction of areas of economic significance	179
9.	Known distribution and areas of possible colonisation in Australia	182
III.	Applied control and remedial measures	183
1.	Utilisation of insect predators	183
2.	Utilisation of Arachnid predators	184
3.	Mechanical and cultural methods of control	185
IV.	General conclusions	186
1.	Economic considerations	187
2.	Ecological considerations	188
3.	Evolutionary considerations	188
V.	Acknowledgments and References	189

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I. Seasonal Variation in Abundance of Smynthurus.

1. Guiding Principles in Selection of Area for Population Census.

Following the method of procedure already outlined, the life-history of *Smynthurus viridis*, its bionomics in *sensu stricto*, and the influence of environmental factors under controlled laboratory conditions, having been considered, the next step is an examination of the seasonal cycle of events as occurring in nature. Part II is, therefore, devoted largely to an analysis of the field data, coupled with an interpretation thereof as substantiated by critically planned and controlled laboratory experimentation; this reinforcement being rendered necessary on account of a multiplicity of factors acting simultaneously in nature. The chief difficulty in an investigation of this kind (as with all problems concerned with fluctuations in the numbers of organisms) lies in the fact that there are few methods for obtaining quickly and easily an accurate quantitative sample of the numbers and kind of organisms; and, secondly, there is the difficulty of finding (in a long-inhabited country like Britain) a "normal" environment, *i.e.*, one in which purely natural agencies have been allowed free play over a sufficient interval of time to allow a state of equilibrium to have become established between the various members of the community to which *Smynthurus* belongs, in their relationship to the physical factors of the environment and to each other.

The reason for carrying out the investigation in a normal environment, as distinct from merely an environment in which the *Smynthurus* population was controlled, was in order to eliminate the effect of cultural practice—a double-edged tool—which may favour the increase of certain species and at the same time eliminate others, so that actually in the original home of an insect its non-appearance in destructive numbers may be due as much to the unconscious efforts of man in his attempts to accommodate the growth of crops as to purely natural factors of control. Further, it is only in such a normal environment that one can be sure of the reproductive potential of the species being in equilibrium with the environment, so that one can validly interpret the variations in the level of the population as due to the pulsation of environmental factors. Not until this equilibrium has been attained can the variations in level of the population be regarded as a true index of the magnitude of the fluctuations in the environmental resistance, although previous to this the fluctuations would doubtless be indicated. These precautions have been amply justified from subsequent experience, and the difficulty of obtaining a representative sample of the population at any time, quickly and easily, in a normal environment has been satisfactorily overcome, owing mainly to the suitability of *Smynthurus* for the purposes of an investigation of this kind.

2. Method adopted in making the Census of Insect Population.

The method adopted was to make a definite number of strokes of the net over a small area (approximately 3 yards × 50 yards) at fortnightly intervals, care being taken to execute the strokes in the same manner, and at the same time of day. It was sometimes necessary to postpone the sweeping for a day or two on account of wet or very windy weather. The plots chosen for the purpose lie in three different fields, known as A, B, and C, and consist of permanent pasture, which has been undisturbed by cultivation for at least 40 years in the case of B and C, and for at least five years in A. While the pasture in C is grazed for the greater part of the year by cattle and horses, B is only grazed during late autumn and early winter by cattle and sheep, and A is ungrazed; so that in A and B we have a very good approximation to a normal environment, and they thus represent almost ideal conditions for the purpose of investigating the seasonal variations, etc., of *Smynthurus*, or any other insect belonging to the grassland community.

The reason for adopting fourteen days as the interval of time between two consecutive sweepings was due to the fact that it was feared that any shorter interval,

such as a week, might interfere with the normal course of events by actually removing too many members of the population, and that this would influence the numbers of the succeeding generation. However, as the sweepings were made fortnightly and the net actually traversed the same piece of ground (within the plot) monthly, the effect on the subsequent generation must be negligible, as any marked local lowering of the population would soon be levelled up again by influx from surrounding areas. After several trials, it was ascertained that 50 strokes of the net secured more than sufficient numbers to reduce the percentage of error involved in the method to a minimum. As a result of this method of investigation there is now available a complete yearly record of the seasonal variation in the *Smynthurus* population as occurring in each of the three fields A, B, and C, and in addition, almost three-fourths of a second year's record, made until the time of the writer's departure for America. The second year's record serves as a check upon the first one, and is valuable for purposes of comparison, since the climatic conditions of no two years are the same.

3. Recording of Fluctuations of Environmental Factors.

In order to determine whether there existed any correlation between the variations in level of the *Smynthurus* population and the fluctuations of environmental factors, both biotic and physical, the monthly census of the entire insect fauna in the respective fields, together with the records of temperature, rainfall, etc., kept at the laboratory, have been utilised, as the plots are all less than half a mile distant. In addition, a Livingston atmometer was set up in the field, and weekly measurements were made of the evaporation. The mean temperature is calculated from measurements made twice daily at 9 a.m. and 9 p.m. (sun-time) for the fourteen days interval previous to the day on which the sweeping was made ; while the mean maximum is taken from daily measurements at 9 a.m. (representing the maximum temperature for the previous 24 hours) and calculated for the corresponding fortnightly interval. All measurements represent shade temperature, the instruments being enclosed in a Stevenson screen. The rainfall for the interval between two consecutive sweepings represents the total rainfall for that period, as calculated from daily measurements, and similarly the atmometric index represents the total evaporation in cubic centimetres of water for the same period, as calculated from weekly measurements.

4. Seasonal Variations of Smynthurus Population in Field B.

The results obtained for Field B are represented in Graph 14, and the following observations will facilitate its interpretation. The data will be found in Table XII. The *Smynthurus* population is represented in actual numbers per 50 strokes of the net. It will be observed that there is a gradual decrease from the time at which a census was first made, namely, on 10th October, till 21st December, after which not a single specimen could be found in the fields until 10th April (the first time they actually appeared in a fortnightly census was 17th April, as they did not occur in the previous census on 3rd April) when nymphs were obtained for the first time since the previous October. After 17th April there is a gradual rise in numbers till 13th June, and subsequent to this the level of the population undergoes a series of violent fluctuations. It now remains to account for these fluctuations, and in this connection both the biotic and the physical environmental factors have to be considered. The latter will be taken first.

A glance at the *Smynthurus* population curve in Graph 14 shows immediately that there are two distinct periods in the seasonal cycle of events ; one in which the course of the population curve is at first gradually falling and then gradually rising, and extending from 1st October (approx.) to 31st May (approx.) ; and one in which the curve undergoes a series of violent fluctuations, extending from 1st June (approx.) to the end of September or thereabout. This suggests that there are two distinct and fundamental influences at work, and this is so. Again looking at Graph 14, it will

be observed that the mean temperature curve may also be divided roughly into two periods; one in which the temperature falls below 45°F., and another in which it exceeds this temperature. The graph also demonstrates conclusively a high degree of correlation between the level of the *Smynthurus* population and the mean temperature, for the first period, and an equally extraordinarily high degree of correlation between the *Smynthurus* population and the rainfall, for the second period, with a



Graph 14. Seasonal variation of *Smynthurus* population.

time-lag effect in the *Smynthurus* curves of 14 days (approx.), which will be accounted for later. It will now be evident that temperature and rainfall are the two fundamental effective factors governing the fluctuations in the *Smynthurus* population, and that temperature is the limiting factor for the first period, while rainfall becomes the limiting factor in the second and short period from approximately June to September (inclusive). How, then, do these two limiting factors bring about their respective effects, and so govern the numbers of *Smynthurus*? In order to understand this it will be necessary to follow in greater detail the actual course of events occurring in the life-cycle in nature, together with the sequence of generations which appear throughout a complete year. The first point to be determined, in order to understand the temperature effect, is the developmental zero of the egg-stage.

5. Developmental Zero and the Concept of Temperature Summation.

As demonstrated by Krogh, Peairs, Shelford, and a few others, the time-temperature curve of development conforms in part to an equilateral hyperbola, so that the reciprocal (for this portion) is a straight line. Hence within the straight line limits of development one may legitimately apply the original phenological conception of temperature-summation, because within this range of so-called medial temperatures (Shelford) the rate of development is directly proportional to the temperature, *i.e.*, the number of effective degrees of temperature (degrees above the developmental zero) $\times$ time $=$ K. The range of temperatures characterised by this hyperbolic rate is usually about a third of the total, and commences about a fifth of the range above the developmental threshold. Hence in attempting to apply this biological phenomenon to the problems of climatology one must remember that the method will only hold good provided that the conditions already postulated do actually obtain, or at least are

TABLE XII.

	FIELD B				FIELD C			
Interval No.	Date	Rainfall (ins.)	Mean temp. (°F.)	No. of Smynth. per 50 strokes	Date	Normal m. temp. Engl. East	Atmom. index	No. of Smynth. per 50 strokes
1	26.9.28	0·16	48·7	—	2.10.28	53·4	—	—
2	10.10.28	0·66	48·9	1659	16.10.28	50·2	—	335
3	24.10.28	2·31	49·1	465	30.10.28	46·3	—	104
4	7.11.28	1·20	43·2	196	14.11.28	44·2	—	48
5	26.11.28	2·51	44·6	55	30.11.28	40·8	—	5
6	5.12.28	0·05	42·0	17	13.12.28	39·3	—	1
7	21.12.28	0·88	33·5	0	4.1.29	37·3	—	0
8	11.1.29	1·89	35·8	0	18.1.29	37·8	—	0
9	23.1.29	0·08	32·0	0	30.1.29	38·3	—	0
10	4.2.29	0·81	36·6	0	14.2.29	38·8	—	0
11	20.2.29	0·18	27·8	0	1.3.29	39·1	—	0
12	6.3.29	0·09	31·5	0	13.3.29	40·8	—	0
13	20.3.29	0·00	37·0	0	27.3.29	42·4	—	0
14	3.4.29	0·04	44·0	0	10.4.29	44·8	252	18
15	17.4.29	0·54	38·7	75	24.4.29	47·0	152	151
16	2.5.29	0·39	41·5	254	8.5.29	49·6	—	720
17	15.5.29	1·37	45·0	678	22.5.29	51·1	193	355
18	29.5.29	1·20	57·1	716	7.6.29	54·5	201	216
19	13.6.29	0·64	55·2	1256	20.6.29	57·4	170	782
20	26.6.29	0·10	58·5	3915	3.7.29	59·9	235	948
21	10.7.29	0·85	56·1	555	19.7.29	60·8	315	—
22	24.7.29	0·07	65·6	1220	2.8.29	61·3	278	23
23	7.8.29	1·64	59·9	140	14.8.29	60·9	194	560
24	21.8.29	0·42	58·2	3340	27.8.29	59·6	245	1315
25	5.9.29	0·08	61·8	1172	11.9.29	57·7	283	110
26	19.9.29	0·00	62·4	511	25.9.29	55·2	150	73
27	4.10.29	1·02	55·1	60	10.10.29	50·5	122	2
28	16.10.29	1·40	52·3	172	23.10.29	48·4	91	262

Interval Number	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Accum. Temp.°F.	68·5	76·4	23·0	49·0	12·0	0·0	6·5	0·0	6·0	0·0	0·0	0·0	20·0	1·0	10·0	33·0

closely approximated. This may partly account for the aspersions frequently cast on the conception of temperature-summation, together with the fact that the idea is not a new one. As in the field of statistics, where results are sometimes obtained which appear to conflict with common sense, the inaccuracy is not usually due to an inherent defect in the statistical formula, but to the inapplicability of the method in that particular field.

The straight line limits of development for the egg of *Smynthurus* have been determined approximately, and would appear to extend over the temperature range 9°–21° C.; this being situated low down on the temperature scale in comparison with most developmental stages which have been investigated, but, as has already been pointed out, all the metabolic activities of *Smynthurus* have this characteristic in relation to temperature. It now remains to be observed whether the temperature experienced out-of-doors during the developmental period of the overwintering egg-stage, namely from October to March in Britain, ordinarily falls within the limits 9°–21° C., in order to enable one to predict with reasonable accuracy the appearance of *Smynthurus* nymphs in spring. In so far as temperatures above 21° C. are concerned, these are easily disposed of, since they do not obtain in Britain during the period under consideration. Now, by projecting the straight line portion of the temperature-velocity curve, it is found that the temperature axis is cut at 7·2°C., which means that one can utilise this temperature as the basis for purposes of summation, although it does not represent the developmental zero of the egg-stage. However, for purposes of practicability and simplicity (the latter being the essence of the former) 7·2° C. has been assumed as the developmental zero, although development in the egg of *Smynthurus* would appear to continue at a perceptible rate down to 5° C. Hence, if outdoor temperatures do not fall between 7·2° C. and 9° C., one can make a fairly good approximation to the probable date of emergence of the *Smynthurus* nymphs in spring, because when below 7·2° C. development is almost inhibited, and when above 9° C. it is proceeding at the hyperbolic rate. Now, using mean daily temperatures for purposes of summation, it is found that slightly under 25 per cent. of the observations fall within the prohibited range, 7·2°–9·0° C.; but this does not mean that they are on that account valueless, although it does mean that our prediction is going to be out somewhat, and the larger the number of observations falling within this non-hyperbolic range, the greater the probable error of our prediction. Putting the above principle into operation, we shall observe by referring to Table XII, where the total number of day-degrees of effective temperature (*i.e.* over 45° F.) for each interval between two consecutive sweepings is indicated, that from 26th September onwards the total heat-energy available falls far below the requirements for complete development of the egg-stage, which necessitates 263 day-degrees (F.) of "medial" temperature, whereas the total accumulated effective temperatures from 26th September to 21st December is only 228·9. The gradual decrease in the *Smynthurus* population from 26th September to 21st December is undoubtedly due, therefore, to the gradual dying out of a generation and its non-replacement by a subsequent generation, on account of an insufficient heat-energy to allow of the complete development of the egg-stage. Any eggs which were deposited after 26th September were, therefore, unable to develop until the following spring. Now the total accumulated effective temperature from the above date to the 20th March is still below the requirements for complete development of the egg, being only 241·4 day-degrees F., but by 10th April this had increased to 261·4, and nymphs emerged on this date. Making allowances for the known shortcomings of the method employed, it will be admitted that the agreement between the calculated and the actual time of emergence is extraordinarily close, the difference being only 1·6 day-degrees Fahrenheit. The writer is fully aware that the conception of a constant sum of effective temperatures has been subjected to much adverse criticism, due to the different effects of constant and fluctuating temperatures, as well as to the fact that the action of one degree of temperature for a known period of time varies slightly at

different temperatures. It must be remembered, also, that the principle only holds good provided that there is no other limiting factor, or if one is present, that it acts with equal intensity throughout the developmental stage, and that the constant sum of temperatures is calculated with reference to this factor. Since the optimum humidity for the various stages in the development of insects is now known to vary tremendously, it seems highly reasonable to suspect that those instances in which the principle gave very inaccurate results may have arisen from neglect of the minimum effective humidity requirements, let alone excessive humidity conditions, which may also slow up metabolism. In any case, the principle is highly adaptable for all practical purposes in this instance.

Before making use of the idea involved in a constant sum of effective temperatures, it was attempted to utilise ordinary and effective temperatures (*i.e.*, taking into consideration only those days in which the temperature exceeded 45 F.) in correlating disappearance and reappearance of nymphs with the seasonal variations in temperature. The results are tabulated below, and from these it will be noticed that in each instance the temperature at which hatching commenced is somewhat lower than the corresponding temperature at which hatching ceased, which is due to the cumulative temperature effect over the long intervening period.

	Mean min. temp.	Mean max. temp.	Mean temp.	Mean effective temp.
Hatching ceased	42·4°F.	62·6°F.	48·9°F.	51·1°F.
Hatching commenced ...	33·0°F.	59·5°F.	44·0°F.	47·7°F.
Difference in temp. ...	9·4°F.	3·1°F.	4·9°F.	3·4°F.

The mean maximum and mean effective temperatures apparently act as the best indices to the actual temperature conditions affecting the development of the egg, and one may say that, in the neighbourhood of the station in which the above temperature records were made, *Smynthurus* nymphs will cease to emerge in autumn when the mean maximum temperature falls below 62·6°F., or the mean effective temperature falls below 51·1°F., while nymphs may be expected in the fields in spring, whenever the mean maximum temperature reaches 59·5°F., or the mean effective temperature reaches 47·7°F. As the above temperatures do not represent the actual temperatures obtaining in the micro-climate of the developing egg they are only of relatively local significance, but once determined for any locality, they serve as a reasonably accurate index to the emergence time of *Smynthurus* nymphs, and render unnecessary the more laborious process of temperature-summation. To eliminate, so far as possible, fluctuations in temperature, it is better to take fortnightly (or better monthly) rather than weekly means, these representing the mean temperatures for the preceding fortnight. The mean temperature for the whole climatic area known as "England E.," under the scheme of the Meteorological Office, was 42·8°F. for the two weeks previous to the emergence of *Smynthurus* nymphs at Farnham Royal in April 1929, while for the corresponding period in April 1930, it was 45·6°F., a difference of only 2·8°F., despite two very abnormal seasons, namely the winter and spring of 1928–29 and 1929–30. The deviation from the mean value at Farnham Royal is almost negligible, so it seems reasonable to conclude that the latter method possesses a very considerable degree of practical utility.

6. Temperature and Rainfall as Limiting Factors to Population Increase.

Emergence of the nymphs in spring marks the commencement of the second part of the first period, during which the *Smynthurus* population steadily rises under the

stimulating influence of a gradually rising temperature, a schematic illustration of the course of events being presented in Diagram A, where the black columns represent rainfall, and white, the numbers of *Smynthurus*, both drawn to the same scale as in Graph 14. A steady rise in numbers occurs till 15th May, due to the gradual emergence of nymphs throughout the period, since temperature is still acting in a highly limiting capacity (see Graph 14), while the rapid rise of temperature during the fortnightly interval ending 29th May causes the appearance of numbers of early nymphs, on account of delayed development on the part of a small proportion of the overwintering eggs. By 15th May, many of the nymphs have reached the seventh

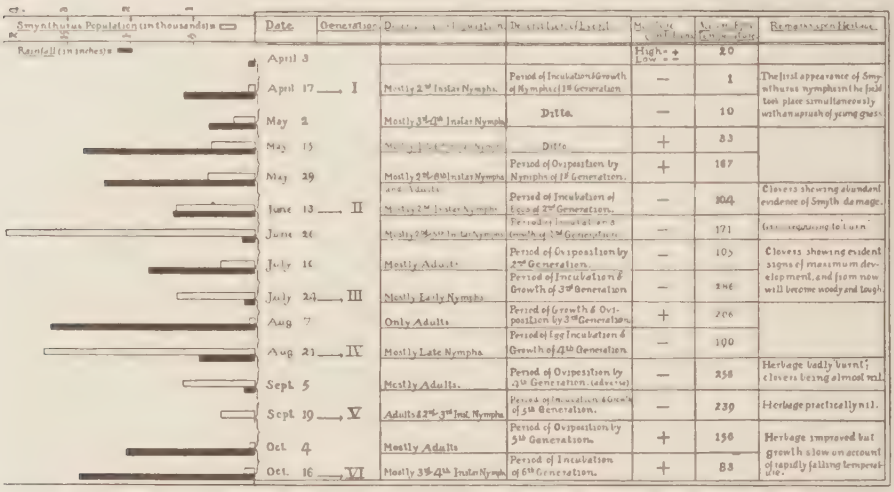


Diagram A. Summary of *Smynthurus* life-history, illustrating relation to environmental factors.

instar, during which sexual maturity is attained, and the period of oviposition by nymphs of the first generation has commenced. In no case has this period of oviposition been defined as the result of direct observation in the field, which would have involved enormous waste of time, but by knowing (i) that oviposition will occur after the attainment of the seventh instar, provided that conditions of temperature, humidity, etc., are suitable, and (ii) the period of emergence of the young nymphs—it is easy to calculate back, by means of the developmental constant, to the exact period during which oviposition must have taken place.

For instance, on 13th June, numerous nymphs of the second generation appeared in the sweepings for the first time, and between 29th May and this date the heat energy available for development of the egg-stage amounted to only 104 day-degrees F., so that oviposition must have taken place prior to 29th May, and since the nymphs had not reached sexual maturity before 15th, oviposition must have taken place between 15th and 29th May. The heat energy for this period is 167 day-degrees F., *i.e.*, just more than enough to allow complete development of the eggs, and the appearance of nymphs on 13th June. Nymphs of this generation continued to emerge up till 26th June, since oviposition was continued over the interval, 15th to 29th May (approx.). This marks the close of the first and the commencement of the second period in the seasonal cycle of events, during which the population of *Smynthurus* undergoes a series of rapid and violent fluctuations correlated with the rainfall, temperature being no longer the limiting factor to population increase.

It may be advisable to state here that by the term " limiting factor " as applied to natural populations, the writer implies that factor which is of preponderating signifi-

cance in comparison with any other single factor inhibiting the rate of population increase. This definition involves the conception that, although there are numerous factors acting simultaneously to reduce the rate of population increase in nature, there is usually one factor of outstanding significance in comparison with any other, and sometimes many or all other factors combined. The writer believes this to be so, the reasons for which will be treated in a subsequent paper. Hence the labours of the economic entomologist, or biologist, must be largely concentrated, to begin with, in determining the "limiting factor," as above defined.

In this instance, temperature still checks the rate of population increase, through the adverse effect of high temperatures upon survival of the early nymphs, and upon the developing embryo in the egg (see later); also to a certain extent indirectly through its effect upon the evaporating power of the air, but temperature is no longer the limiting factor to population increase. In the discussion of this second period it will be unnecessary to describe at length the course of events in each successive generation, since these are presented in more or less detail in Diagram A. All that will be attempted, therefore, is a consideration of the successive generations in their relation to each other, and as a combined expression of the inevitable reaction of numerous individual organisms to a complex of environmental stimuli, the most important of which is atmospheric and soil moisture. Looking at Graph 14, in this second phase, what immediately strikes the eye is the extraordinarily high degree of correlation between rainfall and numbers of *Smynthurus*, bearing in mind that there is a time-lag effect of approximately 14 days, so that the total rainfall for any fortnight is correlated with the *Smynthurus* population at the end of the following fortnight. This extraordinarily close correlation is not mere chance coincidence, but is the logical and necessary result of the synchronisation between life-cycle and the limiting factor in the environmental complex. How, then, does this limiting factor (rainfall) regulate the "timing of events" during the second period of the seasonal cycle, as well as the magnitude of the *Smynthurus* population?

7. Criteria of Significant Factors in Analysis of Environment.

In order to determine this it is necessary to analyse a maze of interlocking and interdependent environmental factors, which operate simultaneously, and on different phases of the life-cycle, with different intensities. Since the method adopted in unravelling what, at first sight, appears to be a bewilderingly tangled skein may be of some interest, it will be described in detail. The procedure consisted of an analysis of the effects of temperature, rainfall, and evaporating power of the air, over the respective generations in the second (and by far the most important) period of the seasonal cycle of events. This was done by breaking up the life-history into its component phases and plotting the response of the phase (*e.g.* oviposition) in each generation, against each of the respective environmental factors, so that in this way the degree of correlation could be assessed by the form of the curve obtained. The best correlation, in the above instance, between any phase and a particular environmental factor will be obtained when the factor in question is acting in a highly limiting capacity, every increment of that factor producing a relatively greater response than the corresponding increment of any other factor during that same period of time. The ecological significance of this is simply that the environment is more deficient in the supply of this factor than of any other factor, relative to the physiological process in question, on account of its peculiar intrinsic requirements.

To carry out such an analysis demands an intimate knowledge of the actual course of events taking place in the field, so that one can determine with accuracy the particular periods of time in which the respective phases occur. Another essential is diversity of environmental conditions throughout the different generations, in order to have a wide range of observations, and in this the writer was fortunate, owing to the abnormal weather conditions of 1929, which presented a variety of temperatures and

rainfalls during the several phases of the respective generations. Proceeding in the manner just indicated, nine different graphs were constructed, plotting the response of the phase on the ordinate against the environmental factor on the abscissa. It is important to note that the measure of response was not the actual population resulting from the operation of a particular factorial intensity, but the ratio of increase or decrease on the already existing population. In assessing the relative significance of the different factors as ascertained from an examination of the graphs above described, these are the main points which require careful consideration ; (i) the form of the curve which produces the best possible fit to our observations, (ii) the degree of adherence of our observations to the curve so obtained, (iii) the relative position of our observations to the total range of response.

TABLE XIII.

Effect of certain Combinations of Temperature and Rainfall upon Oviposition by Smynthurus

Period (14 day) ending	Oviposition period	Rain-fall (ins.)	Mean temp. F.	Mean max. temp.	Smynth. popula-tion	Ratio of increase	Order of favoura-bility
29.v.29	Of 1st genrn.	1·20	57·1	69·5	3915	716:3915 (1:5·4)	(2)
10.vii.29	,, 2nd ,,	0·85	56·1	66·8	1220	555:1220 (1:2·2)	(4)
7.viii.29	,, 3rd ,,	1·64	59·9	69·0	3340	140:3340 (1:24·0)	(1)
5.ix.29	,, 4th ,,	0·08	61·8	77·0	511	1172:511 (1:0·4)	(5)
4.x.29	,, 5th ,,	1·02	55·1	66·2	172	60:172 (1:2·8)	(3)

Effect of certain Combinations of Temperature and Rainfall upon Emergence of Smynthurus *Nymphs.*

Period (14 day) ending	Incubation period	Rain-fall (ins.)	Mean temp. F.	Mean max. temp.	Smynth. popula-tion	Ratio of increase	Order of favoura-bility
26.vi.29	Of 2nd genrn.	0·10	58·5	69·0	3915	716:3915 (1:5·4)	(2)
24.vii.29	,, 3rd ,,	0·07	65·6	80·4	1220	555:1220 (1:2·2)	(3)
21.viii.29	,, 4th ,,	0·42	58·2	72·8	3340	140:3340 (1:24·0)	(1)
19.ix.29	,, 5th ,,	0·00	62·4	75·6	511	1172:511 (1:0·4)	(4)

Effect of certain Combinations of Temperature and Rainfall upon Survival of Early Nymphs of Smynthurus.

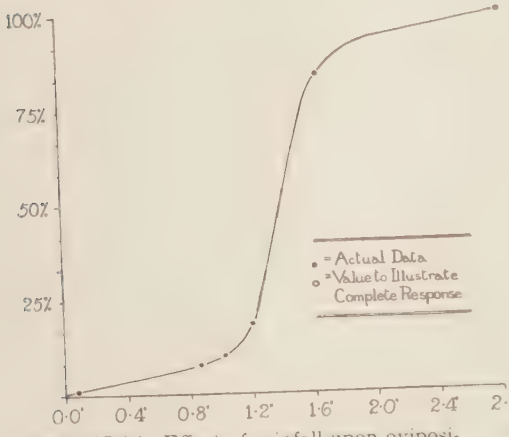
Period (14 day) ending	Growth period	Rain-fall (ins.)	Mean temp. F.	Mean max. temp.	Smynth. popula-tion	Ratio of decrease	Order of favoura-bility
26.vi.29	Of 2nd genrn.	0·10	58·5	69·0	555	3915:555 (1:0·14)	(2)
24.vii.29	,, 3rd ,,	0·07	65·6	80·4	140	1220:140 (1:0·11)	(4)
21.viii.29	,, 4th ,,	0·42	58·2	72·8	1172	3340:1172 (1:0·35)	(1)
19.ix.29	,, 5th ,,	0·00	62·4	75·6	60	511:60 (1:0·12)	(3)

Bearing this in mind, out of the nine graphs constructed, two have been selected as representing the most important physical factors in the control of the *Smynthurus* population, and these are presented in Graph 15, the data being supplied in

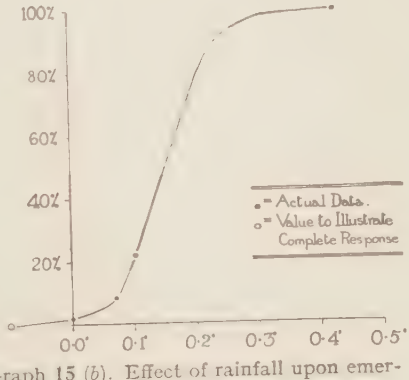
Table XIII. Examination of the data, facilitated by the graphical illustrations, indicates that the relative importance of the different factors, and their mode of operation, in checking the natural increase of the *Smynthurus* population is as follows :—(*a*) the effect of rainfall upon oviposition, (*b*) the effect of rainfall upon development and emergence of nymphs from the egg, (*c*) effect of temperature upon development and emergence of nymphs from the egg

8. Effect of Rainfall upon Oviposition.

The reasons for the above selection are briefly these. Firstly, in Graph 15 (*a*) all the observations fall on the theoretically best fitting curve, and the latter assumes the typical sigmoid form of population increase curves ; the first point indicating that we are, in this instance, dealing with a " dominating reaction " or " master effect " which cannot be subjugated by the preponderating influence of any other environmental factor, and the second point acting as a reinforcement to the conclusion that we have here a real effect and not merely an artefact. Further, out of the five observations, four fall below the mid-point of inflexion of the curve, showing that conditions of rainfall during the oviposition period throughout the five generations



Graph 15 (*a*). Effect of rainfall upon oviposition.



Graph 15 (*b*). Effect of rainfall upon emergence of nymphs.

were, with one exception, far removed from conditions productive of the maximum response, more so indeed than those for any other phase in the life-cycle. This is, of course, due to the intrinsic requirements of the oviposition process in *Smynthurus*, involving a very high rainfall during its progress, so that the demands of this vital process upon the environment (if the reproductive process is to give rise to its fullest expression) are such that the latter is less able to fulfil these requirements than those of any other of the vital processes in the life-cycle. The necessity of a high rainfall during the oviposition period is undoubtedly associated with the peculiar habit of the insect, in that it covers each egg with an exudate of soil passed via the anus. To this end, an enormous amount of soil has to pass through the alimentary tract, and unless the soil be in a very moist condition the insect is incapable of eating the necessary quantity. The following simple experiment was conducted to demonstrate this point. Forty adults were collected from the field and equally distributed to four glass petri dishes as follows : (i) provided with dry filter paper ; (ii) provided with filter paper kept continuously moist ; (iii) provided with powdered dry soil of pH 6·5 (*i.e.* almost optimum pH) ; (iv) provided with the same type of soil, but kept constantly saturated with distilled water. All four

were supplied with fresh green clover leaves, and at the end of five days the number of eggs produced in each lot was counted and found to be as presented below :

	Without moisture	With moisture
Without soil ...	(i)—0	(ii)—11
With soil ...	(iii)—0	(iv)—99

This confirms the suggestion of Holdaway that the presence of soil has a stimulating effect upon oviposition in the case of females ready to lay eggs, and also demonstrates that, in addition, a certain moisture content of the soil is essential before oviposition will take place. The exact amount of moisture necessary will vary with different types of soil, depending upon its saturation capacity, as determined by the texture and structure of the soil-type. In any case it is very high, and would appear to be almost 100 per cent. saturation for maximum oviposition.

9. Effect of Rainfall upon Development and Emergence of Nymphs.

Continuing the analysis of the physical environment, the next most important controlling factor of the *Smynthurus* population is the effect of rainfall during the development and the emergence of the nymphs from the eggs, as presented in Graph 15 (*b*). Here we must make allowance for a slight artefact, as indicated by the emergence of a small population when the rainfall is nil. This is due to the fact that when the moisture requirements for maximum response are so small (as in this instance) the effects of dew assume very considerable significance, although unrecorded. The well-known dew-ponds of the chalk Downs afford a good illustration of the amount of water vapour deposited in this form, even when the rainfall has been negligible over long periods. Three of the observations fall below the mid-point of inflexion of the curve, but these are not so far removed from the maximum response as indicated by the curve, *i.e.*, if we consider a rainfall of nil as the zero, but if we take the point where the projected curve cuts the rainfall axis as the zero, then we obtain the true measure of departure of our observations from the maximum response. The mode of operation of rainfall upon the developing egg of *Smynthurus* is bound up with the question of atmospheric humidity in the micro-climate, the relative humidity as recorded in the Stevenson screen being too far removed from the actual conditions obtaining in the immediate environment of the egg to have much value for comparative purposes, since the relative humidity in proximity to the ground surface depends to such an extent upon the nature of the substratum. However, experiments conducted with a view to determining the actual effect of various relative humidities upon the partly developed eggs will be considered later in this section, together with the effect of temperature upon the same stages.

10. Effect of Temperature upon Development and Emergence of Nymphs.

The third significant factor controlling the *Smynthurus* population is the effect of temperature during the development of the egg, and in this respect the evidence drawn from the field data indicates that up to a daily mean temperature of 58·0°F. the destruction of partly developed embryo nymphs, due to the adverse effects of high temperatures, is negligible, but that above this temperature there is a profound and rapid reduction in the numbers of nymphs which emerge from the egg-stage. The effect continues with increasing intensity up to 66°F. (approx.), when the numbers escaping destruction become practically nil. Experiments conducted in the laboratory to determine the exact effect of temperature (and various combinations of temperature with different relative humidities) on the partly developed eggs of

Smynthurus gave the following significant results. The several associations of temperature, humidity, and time of exposure were so arranged as to approximate conditions actually obtaining in the field; since, in order to throw some light on the mortality effects of these factors in nature, it was obviously useless to subject the developing egg to artificial climatic conditions which were not approximated in the field, interesting though they might be from a purely scientific standpoint. The factor intensities and exposure periods were taken from a hygro-thermograph chart record and slightly modified to facilitate experimental procedure, the modification always being made in a direction favourable to increased survival, so that conditions in the field are, if anything, occasionally more severe than those indicated. The conditions presented in Experiment No. 3, however, are seldom approximated in Britain for any length of time.

Series of Experiments to determine the Effect of fluctuating Conditions of Temperature and Humidity upon the Percentage Hatch of partly developed Eggs of Smynthurus.

The eggs had completed 80–85 per cent. of their total development and were subjected to the following conditions for a period of 10 days, after which they were transferred to an environment highly favourable for the completion of their development, and the percentage which emerged was noted.

Exp.	Time interval	Environmental conditions	Percentage emergence (highest ever obtained at time indicated)
No. 1	9 p.m.—9 a.m. ...	12 hrs. @ 16°C. and 100% R.H. ...	28% in 180 hours, 48% in 204 hours; 62% in 228 hours; 66% in 276 hours.
	9 a.m.—9 p.m. ...	12 hrs. @ 21°C. and 85% R.H. ...	
No. 2	9 p.m.—9 a.m. ...	12 hrs. @ 16°C. and 100% R.H. ...	4% in 228 hours.
	9 a.m.—11 a.m. ...	2 hrs. @ 21°C. and 85% R.H. ...	
	11 a.m.—7 p.m. ...	8 hrs. @ 25°C. and 60% R.H. ...	
	7 p.m.—9 p.m. ...	2 hrs. @ 21°C. and 85% R.H. ...	
No. 3	9 p.m.—9 a.m. ...	12 hrs. @ 16°C. and 100% R.H. ...	Nil.
	9 a.m.—11 a.m. ...	2 hrs. @ 21°C. and 85% R.H. ...	
	11 a.m.—12.30 p.m. ...	1½ hrs. @ 25°C. and 60% R.H. ...	
	12.30 p.m.—5.30 p.m.	5 hrs. @ 29°C. and 50% R.H. ...	
	5.30 p.m.—7 p.m. ...	1½ hrs. @ 25°C. and 60% R.H. ...	
	7 p.m.—9 p.m. ...	2 hrs. @ 21°C. and 85% R.H. ...	

The above experiments clearly demonstrate the adverse effects of high temperatures in conjunction with low humidities on the developing egg of *Smynthurus*. The conditions presented in Experiment No. 1 are often exceeded in intensity in Britain during the summer and early autumn months, and those presented in Experiment No. 2 are not uncommon in late summer and early autumn but do not exist for as long as 10 days in succession. An environment of 100 per cent. R. H. and a temperature of 16°C. is highly favourable for development of the egg. In connection with

these adverse effects it must be borne in mind that the eggs are deposited on the soil surface or amongst the vegetable debris which tends to accumulate therein, and it will therefore be necessary to consider briefly the ecological peculiarities of this habitat.

Studies by Buxton, Chapman, and Williams have shown that the sand surface in desert areas is characterised by violent diurnal fluctuations in temperature. The same holds good, however, for the soil surface in temperate regions, although the amplitude is not so great. Analysis of the records made under the meteorological scheme of the Ministry of Agriculture and Department of Agriculture for Scotland, shows that from May to August the mean daily air temperature is considerably lower than the mean daily soil temperature, even at a depth of four inches, by which time the temperature effect has been much reduced in the course of penetrating the upper four inches of soil. During the same period the difference between the mean maximum and the mean minimum at four inches is at its highest, being about 20°F. Since it is known that the reduction in amplitude of the soil temperature wave with increase in depth approximates to a relationship such that the amplitude decreases in geometrical progression as the depth increases in arithmetical progression, it follows that the amplitude of soil surface temperatures, even in temperate regions, is very considerable, and awaits detailed investigation. Now the mean maximum temperature at Farnham Royal during the incubation period of the second, third, fourth, and fifth generations was 69°, 80·4°, 72·8° and 75·6 F. respectively. The significance of this in relation to *Smynthurus*, since the eggs are deposited on the soil surface, is obvious, especially in view of the results obtained in the preceding laboratory experiments on the effect of fluctuating conditions of temperature and humidity upon the developing egg. The fact that the eggs are deposited on this physically unfavourable substratum is undoubtedly associated with the primitive nature of the insect, for even if they were deposited a few inches above the soil surface among the herbage they would be subject to less violent temperature variations, while if deposited somewhat below the surface the eggs would also be in a less variable environment and have an increased supply of moisture. Ecologically, therefore, an exposed soil surface is the most primitive of terrestrial habitats, but as the covering of herbage increases in density conditions become more favourable for existence, largely owing to the tendency of the former to damp down violent oscillations of physical environmental factors. The insect also illustrates " the return to the primitive " during periods associated with reproduction (this being usually the last to yield to evolutionary change), since the actively growing nymphs spend most of their time up amongst the herbage, returning only occasionally to browse on the soil surface. The fact that there is a pronounced temperature gradient of decreasing magnitude from the soil surface upwards during the warmest period of the year explains why the mortality amongst the embryo nymphs is heavier than amongst the newly emerged and early nymphal instars, although their physiological requirements as regards temperature and humidity are much the same, the latter being able to escape the unfavourable conditions on the soil surface by climbing a few inches upwards amongst the herbage. On very hot days, the writer was surprised to find many *Smynthurus* poised on the very tip of grass stems (as if they were attempting to climb upwards as far as they could) and was unable to account for this peculiar behaviour until the explanation above was discovered.

Since humidity might be a serious mortality factor in Britain during a wet season, and in certain tropical areas of the world, it seemed desirable to determine the effect of high temperatures upon partly developed eggs in a saturated atmosphere, to which end the following experiments were performed. Eggs which had completed approximately 64 per cent. of their development were subjected to temperatures of 25°C. and 29°C., and allowed to remain there until the nymphs emerged, with the following results. At 25°C., 76 per cent. emerged in 108 hours, 80 per cent. in 132 hours, and 84 per cent. in 156 hours ; and at 29°C., the emergence was 44 per cent. in 108 hours

and 52 per cent. in 132 hours. A control at a mean temperature of 16° C. gave 100 per cent. emergence in 252 hours. Hence it is evident that soil-surface temperatures exceeding 25° C. will have a considerable mortality effect on the partly developed eggs of *Smynthurus*, even in the presence of favourable (*i.e.* high) humidity conditions, and will come into operation in Britain in all but very cool summers.

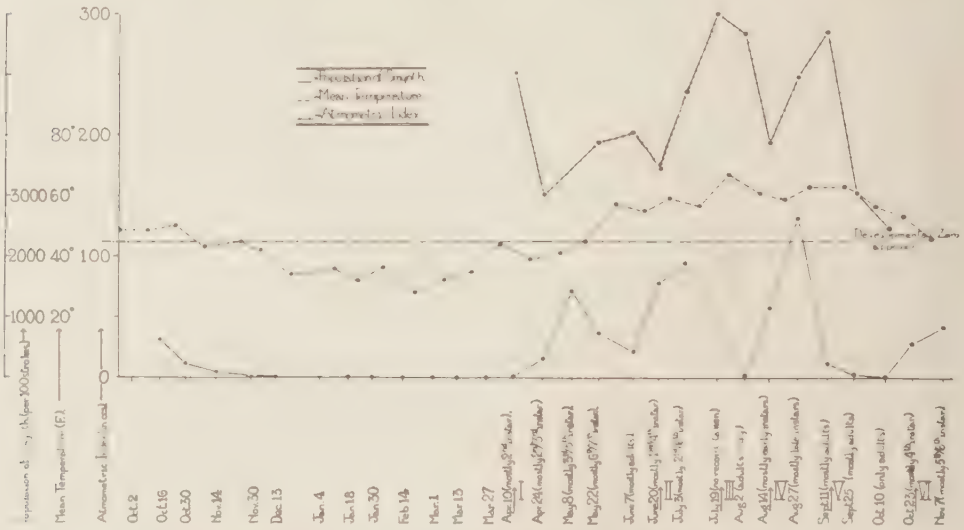
11. Effect of Temperature upon Survival of the Early Instar Nymphs and Adults.

The fourth factor, in order of significance, controlling the *Smynthurus* population, is the adverse effect of high temperature upon survival of the early instar nymphs, which are much more sensitive than the adults. Analysis of the field data in the manner already described shows that daily mean temperatures above 60° F. are very unfavourable for survival of the young nymphs, and that there is a very rapid reduction in the number of survivors as the temperature increases beyond this mean until the attainment of 70° F., when the survival is nil. This temperature effect upon the young nymphs takes place even in the presence of optimum humidity conditions and is intensified when the humidity is lowered. It must be borne in mind that the above temperatures are mean temperatures recorded in a screen four feet above the ground, so that the actual temperatures experienced by the nymphs, for about six hours of the day, are considerably higher. To illustrate concretely the mortality effect of various temperature-humidity combinations, a series of experiments were conducted in which adults were used, being much more convenient for experimental purposes than the young nymphs, which are so small and not always easily obtainable in the large numbers required for these experiments. Bearing in mind that the nymphs are more sensitive than the adults to adverse temperature-humidity conditions, the following results demonstrate the high mortality brought about by comparatively moderate temperatures and humidities such as 80 per cent. R.H. and 30° C. The results are presented below, while those for the "Flea Beetle," *Longitarsus melanocephalus*, have been added as an interesting comparison, as it is one of the dominant species occupying the same habitat as *Smynthurus*.

	10% R.H.	40% R.H.	80% R.H.	100% R.H.	Species.
30°C.	20% in 1 hour 60% in 3 hrs. 100% in 5 hrs.	20% in 1½ hrs. 60% in 4 hrs. 100% in 7 hrs.	20% in 4 hrs. 60% in 30 hrs. 100% in 51 hrs.	20% in 6 hrs. 60% in 30 hrs. 100% in 75 hrs.	*Smynthurus viridis*
35°C.	20% in ½ hr. 60% in 2 hrs. 100% in 4 hrs.	20% in 1 hr. 60% in 3 hrs. 100% in 5 hrs.	20% in 1½ hrs. 60% in 3 hrs. 100% in 9 hrs.	20% in 2 hrs. 60% in 6 hrs. —	*Smynthurus viridis*
40°C.	20% in 10 min. 60% in 25 min. 100% in 1½ hrs.	20% in 20 min. 60% in ½ hr. 100% in 2 hrs.	— 60% in 45 min. 100% in 2½ hrs.	20% in ½ hr. 60% in 1½ hrs. 100% in 3½ hrs.	*Smynthurus viridis*
40°C.	20% in 2 hrs. 60% in 2¾ hrs. 100% in 3½ hrs.	20% in 3 hrs. 60% in 4¾ hrs. 100% in 6½ hrs.	20% in 3¾ hrs. 60% in 5½ hrs. 100% in 8 hrs.	20% in 4½ hrs. 60% in 6½ hrs. 100% in 9 hrs.	*Longitarsus melanocephalus*

It is evident that the mortality effect of temperatures over 30° C. accelerates very rapidly with rise of temperature and decrease of relative humidity. A saturated atmosphere delayed the onset of death longer than any other humidity investigated, including 90 per cent. R.H., so that if there is a humidity more favourable to the prolongation of life at those temperatures it must lie between 90 and 100 per cent. saturation; but the writer is not inclined to the belief that there is such an optimum (between 0 per cent. and 100 per cent.) for *Smynthurus* when temperatures above 30°C. are involved, or for temperatures approaching the limits of tolerance in the

case of other insects. The reasons for this are of somewhat theoretical interest and will not be discussed here. The above may appear contradictory when it is recalled that definite optima below 100 per cent. saturation were obtained for growth and reproduction, but it may be worth while to emphasize that the resistance of protoplasm to adverse temperatures is a signally distinct phenomenon from normally proceeding physiological processes. As regards *Longitarsus melanocephalus*, the resistance of this species to high temperatures is considerably greater than that of *Smynthurus*, although both species are among the predominating ones in a grassland community investigated by means of a monthly census.



Graph 16. Seasonal variation of population of *Smynthurus*—field C.

During the winter months, if temperatures below freezing point prevail for any length of time, the *Smynthurus* die off fairly rapidly, but this effect is apparently due as much to the gradual drying out of the atmosphere which takes place during long spells of frosty weather as to the adverse effect of the low temperature, since they move about and feed, although sparingly, at 0°C., provided that the atmosphere remains very humid, as the following experiments show. Adults maintained at 0°C. and 10 per cent. R.H. were all dead within 24 hours, while at 60 per cent. R.H., at the end of two weeks, there was 20 per cent. mortality, and at 80 per cent. R.H. there was 10 per cent. during the same period. At 3°C. the insects move about and feed, provided that the relative humidity remains above 80 per cent., but they eventually succumb to adverse secondary effects, such as bacterial and fungous attacks, on account of the excessive lowering of metabolism and gradual reduction of general vitality. Oviposition occurs at 3°C., but the number of eggs produced is only about 10 per cent of the maximum, and no eggs were ever obtained at 0°C.

Whilst there is a high negative correlation between the size of the *Smynthurus* population and the atmometric index, the relation between the latter and any particular phase in the life-cycle is not so apparent, since the atmometric index is compounded of several factors which tend to mask any single factor effect. Hence to demonstrate a correlation between a particular phase and the atmometric index, the latter has to be analysed into its several components (*i.e.* the various factors affecting it) and then subjected to the procedure already indicated. Since the factors concerned are mainly those which we have been examining, it will be unnecessary to repeat the process. The pronounced negative correlation between the size of the

Smynthurus population and the atmometric index is clearly demonstrated in Graph 16, the effect being operative only during the second period in the seasonal cycle of events, with a time-lag effect of approximately fourteen days, similar to that for the rainfall curve.

12. The "Timing of Events" in the Life-cycle.

Having now discussed in some detail the major physical factors controlling the *Smynthurus* population one can return to the problem of "the timing of events" in the life-cycle. An examination of Diagram A shows that each fortnightly interval marked "Period of Oviposition" is usually accompanied by a plus sign in the following column, indicative of high moisture conditions throughout this period. The term "high moisture conditions" is purely relative and is taken from the position on the graph showing the oviposition response to rainfall, at which the curve turns sharply upwards. Hence, although relative, the phrase is by no means arbitrary, being indicative of certain minimum rainfall requirements which must obtain before any appreciable response, on the part of the oviposition process, can take place, and below which the ratio of the actual to the maximum organic response is not more than 1 : 10. This amount of rainfall is not a fixed quantity, since it will vary somewhat with different types of soil, depending upon its saturation capacity, but in the environment investigated it is approximately one inch of rainfall in 14 days throughout the period of oviposition. Each interval marked by a minus sign indicates that less than a total of one inch of rain fell throughout the period, and it will be observed that each "Period of Egg Incubation" almost invariably coincides with a period of "low moisture" conditions. This is not mere chance coincidence, and requires an explanation.

Now, it has already been shown, from the laboratory experiments and field data, that sexually mature individuals of *Smynthurus* will only oviposit above certain minimum moisture requirements, and that for anything approaching to normal oviposition to take place those moisture requirements are relatively high, *i.e.*, in comparison with any other phase in the life-cycle. Hence the period of oviposition tends to become synchronous with a period of high moisture conditions, and this is apparently the most important way in which the environment exerts its "timing effect" upon the life-cycle during the second, and most important, period in the seasonal cycle of events. Should the necessary moisture be unavailable at the time of sexual maturity, oviposition is delayed, just as absence of soil brings about a delay in the process; the delay is not of long duration, however, and if oviposition has to take place under adverse conditions of soil moisture, the effect is seen in an enormous reduction in the number of eggs laid, *e.g.*, the oviposition periods of the second and fourth generation, namely, the fortnightly intervals ending 10th July and 5th September respectively.

Temperature is, of course, the most important "timing factor" during the first period in the seasonal cycle, because it not only determines when the first generation shall emerge in spring, but it also determines the time (as well as the amount) of oviposition by the last generation in late autumn, namely when (and by how much) soil surface temperatures rise above 3° C. Throughout the seasonal cycle of events, therefore, the life-cycle of *Smynthurus* becomes synchronised with the limiting factor in the environmental complex, through the timing effect of temperature upon oviposition during the first period, and of rainfall during the second period. That the timing and limiting factors are identical categorically in this instance is purely fortuitous; they differ widely in their implications, the former involving a threshold of organic response to an environmental factor, and the latter, degree of intensity of operation of a factor which may or may not be the same. The difference between the two is of fundamental ecological significance.

A stage has now been reached in this ecological study of *Smynthurus* in which it can be said that, so far as the evidence goes, the physical environmental factors appear to be the major ones concerned in checking the natural increase of the *Smynthurus* population; and as no significant correlation, positive or negative, has been obtained between the numbers of *Smynthurus* and those of any other biotic factor in the natural environments investigated in the neighbourhood of the laboratory, one may say with certainty that in those areas, at least, the physical factors are the only ones exerting a significant control over the increase of the *Smynthurus* population. It would be foolish, however, to attempt broad generalisations and to conclude from the above that biotic factors are seldom of any consequence in controlling the increase of *Smynthurus*, since the areas investigated were undoubtedly small and we may, as a matter of pure chance, have hit upon some which were inimical for peculiar reasons to the survival of a large predator population. Hence the question of biotic factors requires further investigation. Moreover, the effect of soil pH value was left out of the discussion, because the departure from the optimum pH of 6·2 was never more than 0·3, which is negligible for all practical purposes in this instance. The latter will be considered first.

II. Geographical Variation in Abundance of Smynthurus.

1. Significance of Soil Reaction in the Distribution of Terrestrial Animals.

It is a matter of general agreement amongst ecologists and other workers concerned, that soil reaction is an important factor in the geographical distribution of plants. In relation to the distribution of terrestrial animals, however, the subject has been comparatively neglected for the obvious reason that animals are not so intimately associated with the soil substratum in the struggle for a livelihood as are plants. Nevertheless, for those species which spend a portion of their life-history in or on the soil, or depend upon the organic matter contained therein as a source of food, the study of soil reaction in relation to distribution merits greater attention than it has received up to now. Perhaps the first indication of the significance of soil reaction in relation to insects was suggested some years ago by Williams as the result of preliminary observations on the froghopper pest of sugar-cane in Trinidad. These suggestions have been followed up by recent workers in collaboration with soil chemists, resulting in a most striking demonstration of the influence of soil reaction on the distribution of this serious pest. In regard to other terrestrial animals, it was found by Arrhenius that earthworms could not live in very acid soils, and that pH 6–7 appeared to be the optimum range; while Atkins & Lebour have shown that there is a definite relation between the soil reaction and abundance of snails, being most numerous in soils of pH 7–8, and those with calcareous shells being limited to the alkaline end of the pH scale.

As a result of controlled experiments in the laboratory, it had been determined (see Part I) that soil pH value has a definite effect on *Smynthurus*, both in regard to growth and reproduction, especially the latter. (The credit for first demonstrating the adverse effect of an alkaline soil on the reproduction of *Smynthurus* belongs to Holdaway.) It thus became desirable to determine whether the effect was of sufficient significance to make itself observable in the size of the *Smynthurus* population under natural conditions, or whether, in the latter instance, the other natural factors of control were capable of operating with an intensity sufficient to dwarf into insignificance any effect of soil pH value, so that the latter would only be observable in insignificant degree when other conditions were at or near their optimum, as obtained in the laboratory experiments. Now, with all field data the chief difficulty

lies in its correct interpretation, owing to the fact that usually numerous variables are simultaneously involved. Hence to reduce the complexity (we cannot eliminate it in nature) to a minimum, the careful investigator must so choose his experimental areas that they approach as nearly as possible to the ideal (laboratory) experiment, in which there is only one variable and a control.

As the variables include such factors as temperature and rainfall, the effect of different cultural measures, rotations, intensity of grazing, etc., the writer had almost despaired of demonstrating by means of field data the rôle of soil pH value in nature. However, the idea of sweeping the "Park Grass Plots" at Rothamsted ultimately presented itself, and it will be admitted that the conditions obtaining there are probably as near an approach to the ideal laboratory experiment with a control and one variable as is possible to obtain under natural conditions. These plots have carried hay each year since 1856; hence the effects of different rotations, grazing intensities, and cultural measures, are eliminated, and as the plots adjoin one another the effect of different climatic conditions is also eliminated. They have, however, been subjected to different manurial treatments, with the exception of two untreated plots which were left as a control. This has produced a differential effect on the bulk and composition of the herbage in the respective plots, which will have to be taken into consideration, but these variables have been rendered capable of quantitative treatment, as careful records of the yield and composition of the herbage are made annually, and were obtained from the monograph of W. E. Brenchley. The different manures have also produced considerable changes in the soil reaction, so that a fairly wide range of pH values is obtainable. The values utilised were those determined by E. M. Crowther from surface samples taken on 27th and 28th June, 1923, in the 78th year of the plot experiments. Although the *Smynthurus* sweepings were made on 15th May, 1930, it is highly improbable that the soil reaction will have changed to any significant extent, since laboratory experiments suggested that *Smynthurus* was not sensibly affected by a change of less than 0·2 on the pH scale. As it was not permissible to tread on the plots the sweepings had to be made along the edges, but this was satisfactorily accomplished. Strokes to the number of 50 were made in each instance. The data are presented overleaf in tabular form :—

TABLE XIV.

No. of plot	Manurial treatment	Soil pH value (surface sample)	Per cent. Leguminosae	Yield of hay in cwt./ac. (over the period 1912–21)	Per cent. of *Smynthurus**
	No nitrogen group				
12	Unmanured	5·63	5·2	12	60
3	Unmanured	5·72	4·5	10	13
2	Unmanured (after dung 1856-63) ...	5·86	4·3	—	1
7	Complete minerals†	5·43	8·7	26	27·5
8	Minerals, without potash	5·67	10·4	17	45
4	Superphosphate	5·69	2·7	17	28
	Ammonia group				
1	=43 lb. N. (after dung 1856–63) ...	4·84	0·0	14	2
9	=86 lb. N. and complete minerals ...	4·04	0·0	32	0
10	=86 lb. N. and minerals without potash	3·90	0·0	22	6
4[2]	=86 lb. N. and superphosphate ...	3·93	0·0	17	1
11[1]	=129 lb. N. and complete minerals ...	3·79	0·0	43	1
	Nitrate of soda group				
17	=43 lb. N.	6·30	0·4	23	34
16	=43 lb. N. and complete minerals ...	5·94	1·2	40	1
	Group with manurial changes				
15	Complete minerals after nitrate of soda (=86 lb. N.) 1858–75	5·54	5·4	—	7
6	Complete minerals after ammon. salts (=86 lb. N.) 1856–68	5·31	11·3	—	35
5[1]	Unmanured, after ammon. salts (=86 lb. N.) 1856–97	4·82	0·4	—	17
	Plots which have received lime				
4[2]L	(for manurial treatment see Amm. group)	4·83	0·0	26	10
10 L	(for manurial treatment see Amm. group)	4·71	0·0	34	10
7 L	(for manurial treatment see No Nitrogen group)	6·68	19·6	32	85
15 L	(for manurial treatment see Group with Manurial Changes)	6·13	—	—	100

* The maximum number of *Smynthurus* was obtained in Plot 15 L. the actual number per 50 strokes of the net being 240.

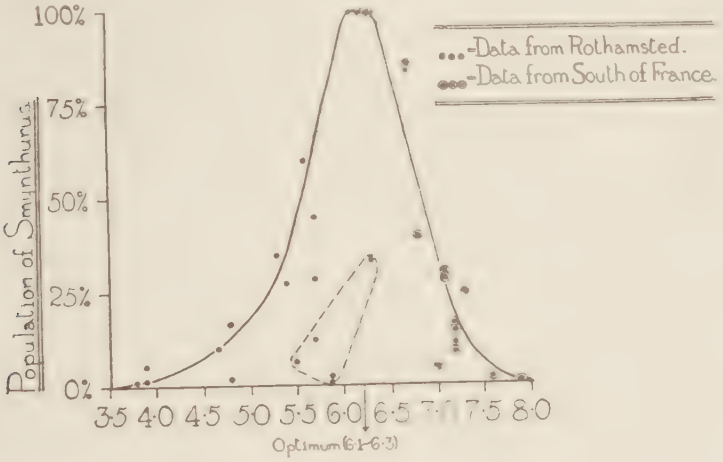
† The complete mineral manure consists of 3½ cwt. Super.; 500 lb. S/POT; 100 lb. S/SODA; 100 lb. S/MAG (all per acre).

As previously explained, the numerous variables usually involved in field data have been largely eliminated in this instance, so that we are only concerned with the effect of the different manurial treatments upon the *Smynthurus* population, brought about through their differential effects upon (1) the soil reaction, (2) the yield, and (3) composition of the herbage. It is therefore necessary to consider separately each of these factors in their relationship to the *Smynthurus* population.

2. Relation between the Smynthurus Population and the Soil Reaction (pH value).

This has been presented graphically by means of a dot diagram (Graph 17), which is a valuable method of rendering visible at a glance, the range and associations of our observations, especially if the latter are not very numerous. The plots at

Rothamsted are nearly all on the acid side of pH 6·2, so that in order to complete the observations a composite diagram has been constructed by utilising data obtained from the South of France, where the soils examined were all fairly alkaline. It has therefore been possible to obtain a range of observations extending from 3·8 to 7·9 on the pH scale, and since the majority of soil types have a pH value somewhere within those limits, the diagram is a fairly inclusive one.



Graph 17. Soil pH value.

It will be observed that :—

(i). There is a short but distinct optimum pH range, extending approximately from pH 6·1 to 6·3, and it is interesting to note in this connection that the optimum both at Rothamsted and in the South of France falls within this range, and, as previously pointed out, the soil pH value regarded as the optimum from laboratory experiments was considered to be slightly on the acid side of 6·5.

(ii). Any departure from this optimum range, either on the acid or the alkaline side, produces a marked decrease in the *Smynthurus* population, the decrease being slightly more rapid on the alkaline side. Soil pH values outside the range 4·5-7·5 are very unfavourable to *Smynthurus*, although by no means inhibitive.

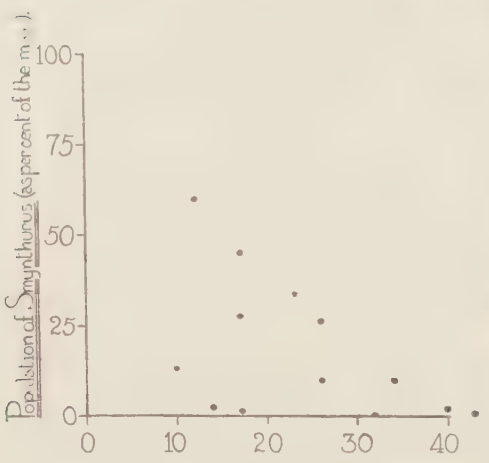
(iii). There are a few exceptions to an otherwise reasonably close correlation and these are enclosed by the broken line. Five observations are here included, being plots 2, 3, 15, 16, 17 ; the first two are unmanured plots and the remainder are all plots which have received nitrate of soda. In all five plots the *Smynthurus* population is lower than one might expect from the soil pH value, but it would appear that different causes are operating, in the first two and last three plots respectively, to bring about a similar effect. It seems that in both of plots 2 and 3 the low *Smynthurus* population follows from a remarkably low yield of herbage, so that the soil surface is exposed to the direct rays of the sun, marked fluctuations in temperature obtaining, with consequent adverse effect upon *Smynthurus* in all stages. On the other hand, in plots 15, 16, and 17, the nitrate of soda has produced a type of herbage, both as regards composition and bulk, which acts as a " blanket " so far as temperature is concerned, but which results in rapid and extensive loss of soil moisture, it being a well known

fact that land under heavy crop tends to dry out much more rapidly than land sparsely covered or under bare fallow. It also affords greater cover for predators. The end result is that in these exceptions we have failed to eliminate the climatic variable, owing to the differential effect of the manures upon the type of herbage, and the microclimate (especially during the hottest months) is very different in these instances.

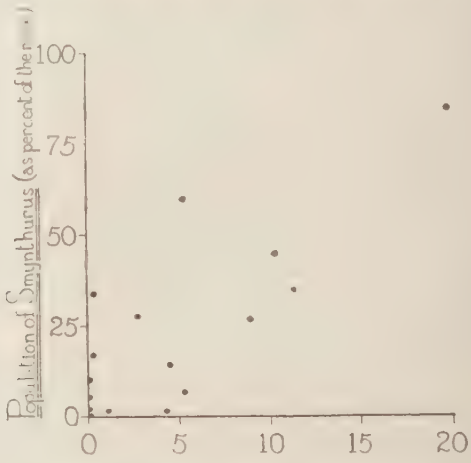
(iv). The subject under consideration in the last paragraph illustrates clearly the "master effect" of climate, so that the effect of soil pH value is always dominated by climatic effects. Hence the greater the departure from the climatic optimum, the less significant does the effect of soil reaction become; while the nearer the climatic factors of the environment approach to the optimum for *Smynthurus*, the greater the significance of differences in soil reaction. In the laboratory experiments, where temperature and humidity conditions were almost at the optimum for *Smynthurus*, the effect of soil reaction obtained for growth and reproduction probably represents the maximum for this effect.

3. Relation between the Smynthurus Population and the Yield of Herbage.

(i). This is presented in Graph 18, and it will be observed that there is evidence of a negative correlation between the yield of herbage and the *Smynthurus* population. This is not due to any relation between soil pH value and bulk of



Graph 18. Yield of hay in cwts. to the acre (over 10-year period 1912–21.)



Graph 19. Percentage of Leguminosae.

herbage, or between yield of hay and percentage Leguminosae, as one might be inclined to suspect, there being no correlation, positive or negative, between these variables, in this instance, and the writer can only explain this correlation as due to the introduction of another variable, namely, the climatic factor. The increased amount of herbage results in more rapid and extensive drying out of the soil, while there is also the possibility of the denser herbage affording greater cover for predators and thereby introducing still another variable.

(ii). Plot 7 L forms a marked exception to this general correlation, and consequently calls for some comment. If we compare this plot with another which has a similar yield and does conform to the above relationship, we can probably arrive at an explanation for the discrepancy. For this purpose we may take plot 10 L. On examining the botanical composition of these two plots we find that there are very

great differences; *e.g.*, in plot 10 L the herbage is of very open nature, consisting of Meadow Foxtail (*Alopecurus pratensis*) to the extent of 76·8 per cent., False Oat Grass (*Arrhenatherum avenaceum*) 8·1 per cent., and only one species outside Graminaceae, namely *Rumex acetosa*, 0·4 per cent., Leguminosae being unrepresented. The remainder is made up of a few grass species, of which *Poa pratensis* and *Festuca ovina* contribute 11·2 per cent. On the other hand the herbage on plot 7 L is of a much closer type, the predominant species being Field Vetch (*Lathyrus pratensis*), which is present to the extent of 19·5 per cent. of the herbage. The predominant grasses are Cocksfoot (*Dactylis glomerata*) 18·6 per cent., and Meadow Foxtail (*Alopecurus pratensis*) 15·2 per cent., with a variety of other grasses, and miscellaneous species other than grasses, in lesser amount, thus presenting a herbage type characterised by the presence of thick bottom grasses completely covering the soil surface. Hence the effects of meteorological factors are modified to a different degree in the two instances, and are apparently responsible for the difference in the populations; on the other hand it might be argued that the larger *Smynthurus* population in plot 7 L is simply due to an increased food supply as represented by *Lathyrus pratensis*, but the writer does not consider this to hold in fact, since *Smynthurus* is by no means entirely dependent upon legumes as a source of food, being able to utilise a large variety of other plants, including mosses and algae, for this purpose.

4. Relation between the Smynthurus Population and the Percentage of Leguminosae in the Herbage.

As regards the food supply of *Smynthurus* the family Leguminosae is undoubtedly the most important, hence it is interesting in this connection to see if there is any relation between the *Smynthurus* population and the food supply. It will be observed from an inspection of Graph 19 that there is a fairly good positive correlation between the percentage of Leguminosae in the herbage and the *Smynthurus* population, but the relationship is not a very close one, and would appear to be due to the fact that there exists some relation between the percentage of legumes and the soil reaction. This latter relationship is, however, not a simple one, different species coming in, and others dropping out, at different points on the pH scale; and as an additional complicating factor there is the suppression of certain legumes, brought about as the result of intense competition with other species especially favoured by a particular soil reaction. It seems, therefore, that food supply seldom acts as a limiting factor to the increase of *Smynthurus* in a natural environment, except in certain abnormal and peculiar instances, where the other factors in the environment are operating at, or near, their optimum for the species, and the struggle for existence then becomes largely a struggle for food.

5. Influence of Biotic Factors upon the Smynthurus Population.

The only definite result concerning the effect of predators on the *Smynthurus* population in nature, which could be ascertained from an analysis of the field data obtained in the neighbourhood of the laboratory, was that when the *Smynthurus* population was high the predator population also tended to be high, and that at no time was there any significant deviation from what one might expect as the result of a good correlation between the *Smynthurus* population and the physical environmental factors already described. In order to obtain corroborative evidence for this result, which might not be of universal application, a number of lucerne sweepings from the South of France were subjected to a rough quantitative analysis, separating out and counting the chief recurring insects and arachnids. The main conclusions are as follows, and these serve to reinforce from a different aspect the principal results already derived from the ecological studies on *Smynthurus* in the South of England.

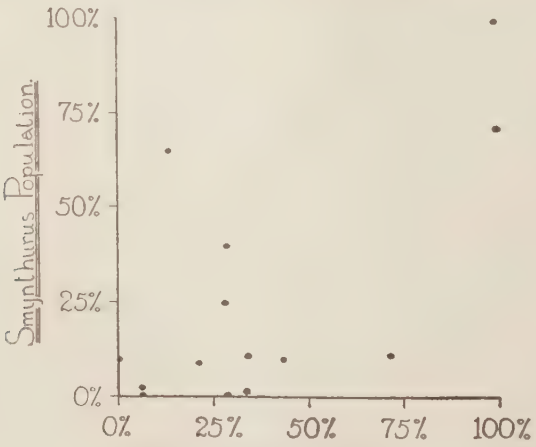
There is no evidence of a correlation, either positive or negative, between the *Smynthurus* population and the total number of other insects or any single family of insects, but there are indications of a fairly good positive correlation between the *Smynthurus* population and the spider population. The data (Table XV) have been depicted graphically by means of a dot diagram (Graph 20).

TABLE XV.

Data from South of France to show Relationship between Soil pH Value, Spider Population, and Population of *Smynthurus*

Smyn. pop. (%)	100·0	11·0	25·0	40·0	9·0	86·0	17·0	0·5	2·0	29·0	100·0	5·0	31·0	15·0	—
Soil pH value	6·3	7·2	7·3	6·8	7·2	6·7	7·2	7·9	7·6	7·1	6·2	7·0	7·1	7·2	—
Spider pop. (%)	—	71·5	28·5	14·0	28·5	100·0	43·0	0·0	100·0	0·0	28·0	28·5	21·5	7·0	7·0
Smyn. pop. (%)	—	11·0	0·0	65·0	1·0	71·5	10·0	12·0	100·0	11·0	25·0	40·0	9·0	0·5	2·0

The diagram indicates that, with some exceptions, there is a reasonably good positive correlation between the *Smynthurus* and spider populations. This may be interpreted in two ways; either that a similar type of habitat is favourable to both insect and arachnid, or the spiders are attracted to the *Smynthurus* as a source of food, but are unable to bring about a significant depletion of their numbers. While the former explanation is to a certain extent true, the latter appears to be the important point and the correct interpretation. In samples 3 and 4 the soil was strongly alkaline, thus accounting for the relatively small number of *Smynthurus* in proportion to the number of spiders present, which were evidently finding some other satisfactory source of food. On the other hand, in samples 6 and 8, the soil conditions were peculiarly favourable to *Smynthurus*. Incidentally, it seems worth while mentioning the fact that where *Smynthurus* was very abundant it was found that *Hypera* larvae (the pest of lucerne known in America as the Alfalfa Weevil) were also present in large numbers.



Graph 20. Spider population.

From general observations in the *Smynthurus* insectary and elsewhere it occurred to the writer that another biotic factor of control, in certain circumstances, consisted in the eating of the eggs (since the latter are scattered about on the soil surface) by

animals whose mode of feeding consists of scavenging along the surface of the soil amongst the layer of decaying vegetable matter and organic debris, which tends to accumulate there. This suggestion was supported by the fact that *Smynthurus* failed to become abundant in the greenhouse, although humidity conditions were very favourable, and though the temperature was somewhat high it did not nearly approach the limits of temperature tolerance by the insect. Examination of the soil surface in the clover plots revealed numerous small Dipterous larvae of the genus *Sciara* (MYCETOPHILIDAE), and Collembola of the genus *Isotoma*. It has been found that both these forms devour *Smynthurus* eggs readily. Now it has been shown, as a result of comparatively recent quantitative studies on the fauna of the soil by workers in Britain, Denmark, and Japan, that the Arthropleon group of Collembola are amongst the most abundant (and often by far the most abundant) of the macro-inhabitants of the soil. However, both *Sciara* and *Isotoma* contain species which are peculiarly sensitive to low humidity conditions, and are consequently inhabitants of damp, moist, situations. Experimental studies by Davies on the sensitivity of Collembola to various relative humidities have shown that the Arthropleon forms are less tolerant of low humidities than the Symphypleon group, and that of all the species investigated *Isotoma viridis* was the most intolerant. The writer has ample reason to confirm this, so that although these saprophagous Collembola must undoubtedly exert a considerable controlling influence, in virtue of their numbers, when climatic conditions are favourable, their action period is extremely limited in nature, on account of their incapacity to withstand relatively slight dessication, whence they are forced to avoid the soil surface and retreat to the cooler and moister conditions obtaining in the superficial layers of the soil.

When put to quantitative trial, the scavenging capacity of these saprophagous Collembola was astounding, organic debris being "cleaned up" with extraordinary rapidity, and leaving nothing but the bare soil and living roots of the herbage. The scavenging action of soil Collembola is undoubtedly one of the important factors in the transformation of organic matter in soil, and has been overlooked or attributed to other agencies. Their rôle in the formation of soil would appear to rank next in importance to the classical rôle of earthworms, first propounded by Darwin.

Still another biotic factor of control, is the destruction of the eggs by fungi which, however, is of very little significance, and only comes into operation under peculiar and exceptional circumstances, in which highly favourable conditions of temperature and moisture are involved. No entomophagous parasites of *Smynthurus* have been discovered.

6. Relative Significance of Factors in the controlling Complex in the South of England.

Having discussed in some detail all the major factors, both biotic and physical, which contribute towards checking the potential increase of the *Smynthurus* population in nature, we have now reached a stage when we may briefly recapitulate the evidence, and give a list of the various factors in their order of decreasing significance. These obtain for the second period in the seasonal cycle of events, temperature being, as already explained, the major controlling factor during the first period from October to May (approx.) on account of its inhibiting effect upon the growth of nymphs and development of the eggs.

(i). Effect of rainfall upon oviposition.

(ii). Effect of rainfall upon development and emergence of nymphs from the egg.

(iii). Effect of temperature upon development and emergence of nymphs from the egg.

(iv). Effect of temperature upon survival of the early instar nymphs.

(v). Effect of temperature upon reproduction.

(vi). Effect of physical and chemical conditions of the soil type upon reproduction.

(vii). Effect of predators upon nymphs and adults.

An interesting phenomenon in regard to these factors of control is that all the major ones are associated with reproduction or the embryonic stages. This is not altogether unexpected, in view of the fact that characteristics associated with reproduction are usually the last to succumb to evolutionary change, are least adaptable, and therefore most susceptible to adverse environmental agencies; whereas with increasing departure from the reproductive phases we encounter stages which become progressively more adapted to withstand "the bludgeonings of chance," and consequently have a lower mortality. Further, we have here an interesting, actual example of natural control by a number of independent factors operating in a sequence, and it has been mathematically demonstrated by Dr. W. R. Thompson that in a controlling complex of this type the ultimate effect of the disappearance of factors is a minimum, those which disappear being largely replaced automatically by the succeeding factors. This means that a natural controlling complex of the type here involved is comparatively stabilised or "buffered," if one may borrow a more apt term from chemistry, and that the amplitude of the environmental fluctuations has to be very considerable before any appreciable change is produced in the size of the population. However, it cannot be too strongly emphasized that relatively large environmental fluctuations do occur in nature, and that the stability above indicated is merely relative to that produced by other types of natural controlling complexes. That is to say, although the system is to some extent self-regulating, the mechanism is far from perfect, and can be readily thrown out of gear if the more sensitive elements in the structure are interfered with, namely, the factors affecting reproduction and the early stages.

Such, then, is the natural controlling complex of *Smynthurus viridis* in the South of England. It must be emphasized, however, that although the end result tends towards a mean on account of the composition (type of factors) and structure (mode of operation of factors) of the complex, the relative significance of the respective factors is continually varying in time and space, and even in one small area the relative significance of the less important factors may be occasionally reversed. What we mean therefore by placing a series of natural controlling factors in order of significance is, that at a particular place the control is of that type, at a particular time or on the average. Now, the writer is somewhat sceptical of the employment of averages in biology, because they are often mere fictions which lead to false assumptions, no matter how satisfying they may be to the aesthetic appeals of the investigator who delights in the production of "smooth curves." Nevertheless, they are sometimes very useful for practical purposes, and it is to this end we must now proceed to utilise them, as exemplified in a bioclimatic study of the insect.

7. Prediction of complete Geographical Range of Existence.

The practical utility of all scientific efforts which involve considerable expenditure of time and energy is dependent to a large extent upon the general applicability of the results. Since the climatological study of *Smynthurus*, about to be described, involves the prediction of the geographical range of the insect, it may be asked by critical and cautious observers, to what extent is such bold generalisation scientifically legitimate? An important part, therefore, of this aspect of the ecology of *Smynthurus* will be the justification for the various steps, and, as far as possible, confirmation of the results. Apart from all results of economic significance which may accrue from carefully conducted climatological studies, the one about to be considered is of particular interest from an academic standpoint, because it is based not only upon data obtained under natural conditions but upon critically planned

laboratory experiments bearing upon the "field physiology" of the insect, so that the degree of conformation of the actual with the theoretical distribution of the insect acts as a good check on the accuracy of the many observations and conclusions made up till now.

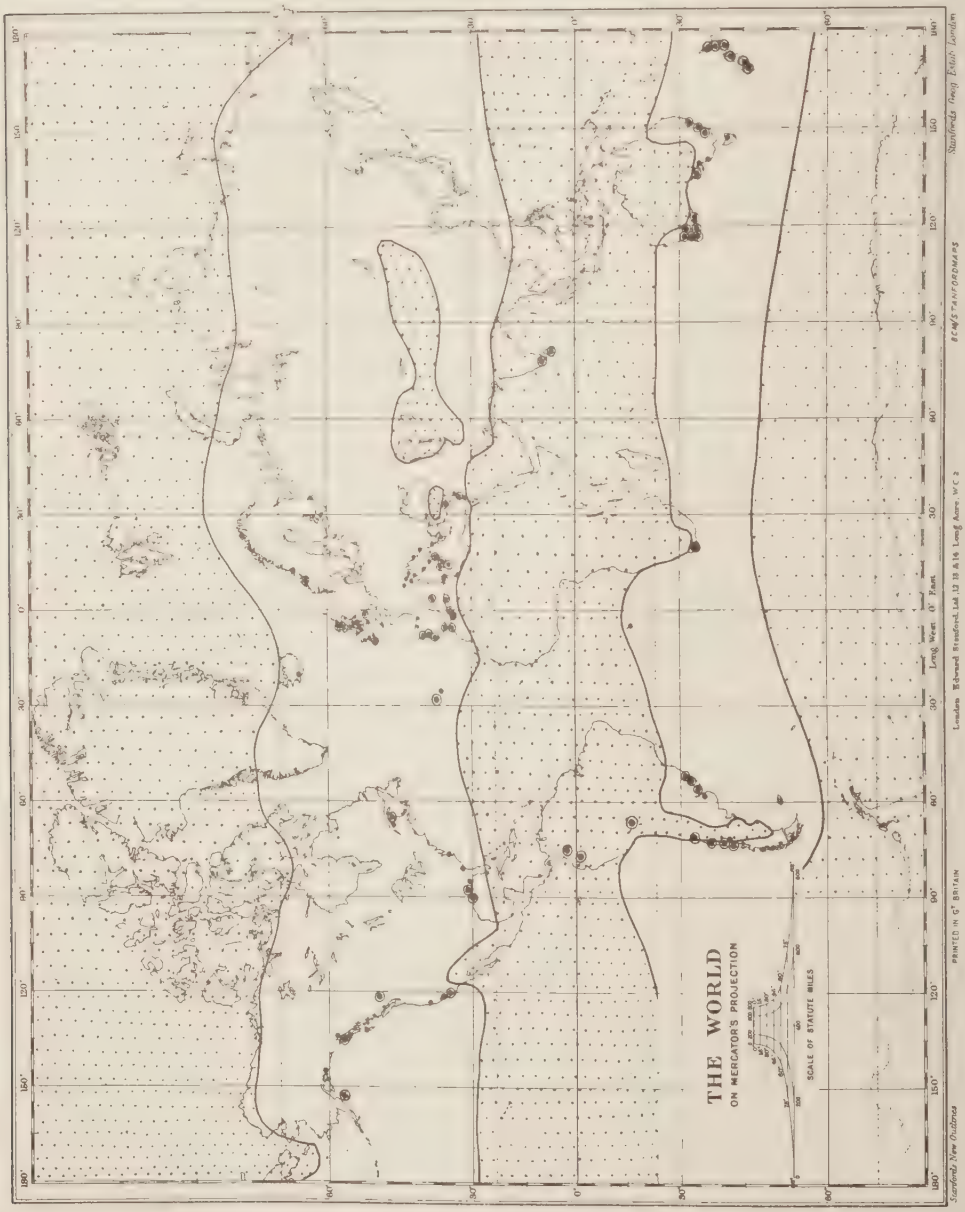
Prior to the commencement of this bioclimatic study of *Smynthurus*, few satisfactory efforts of this type, in relation to animal abundance and distribution, had been attempted, the methods adopted being generally of a somewhat empirical nature; for example, contrasting the climate of "controlled" and "outbreak" areas by means of the shape and position of their respective climographs or hythergraphs, often with little or no exact quantitative evidence of climatic effects upon the various phases of the life-cycle, to reinforce results obtained from an essentially empirical basis. Further, while the climograph method is very useful for comparing or contrasting the favourability or unfavourability of particular climates in connection with insects or other animals whose life-history extends over the whole year (and hence the deviations of any one of the twelve points may be of significance), the utility of this method is greatly diminished with a species which may have as many as five generations in six months. By far the best work of this type, of which the writer is aware, is that of Cook on the Pale Western Cutworm (*Porosagrotis orthogonia*), although very valuable work of a more general nature has been conducted by Bodenheimer in connexion with several insect species.

The bioclimatic study of *Smynthurus* was conducted primarily with a view to determining, if possible, the following three relations: (i) the various parts of the world in which *Smynthurus* could exist; (ii) the localities in which *Smynthurus*, if present, would be likely to cause damage of economic significance every year, at some period of the year; (iii) those parts of the world in which *Smynthurus* would not usually be of economic importance, but might become so occasionally, namely, whenever the climate of the particular locality deviated from the normal, or average, in a direction favourable to the insect. As already pointed out, another important aspect of this bioclimatic study is that it serves to check the accuracy of the numerous points brought forward and discussed in the previous part of this paper.

In the task of elucidating the three relations indicated above, the first step was to determine the limits of heat and moisture under which *Smynthurus* could exist, and then translate these limits into convenient meteorological terms of temperature and rainfall. After investigation into the available meteorological records throughout the world, it was decided to utilise the mean monthly temperature and the total monthly rainfall, more detailed information not always being obtainable. Now from what has been said in connection with the natural factors of control, it will be evident that the minimum rainfall for existence of the species is the minimum rainfall under which oviposition can take place. This has been determined as 0·12 inches a month. By referring to Graph 15 (*a*), in which the rainfall is represented as the total per 14 day interval, it will be observed that 0·06 inches of rainfall would allow the existence of a very small population, but at tropical and sub-tropical temperatures the effective action of this small rainfall would be very greatly reduced on account of the increased saturation capacity of the air. Since it is only being attempted to represent conditions on the average, the selection of 0·12 inches of rainfall a month as the minimum rainfall for the existence of *Smynthurus* seems justified. The other rainfall limit is alternately continual submergence, but adverse secondary effects, due to fungous and bacterial attacks on the eggs and young nymphs, come into operation before this stage is reached, making the upper rainfall limit approximately 7·0 inches.

In regard to temperature, the maximum for the species is the maximum which can be tolerated by the stage least tolerant of high temperatures, and these are the embryonic nymphs, which cannot survive mean temperatures exceeding 66°F. The other temperature extreme is determined by the stage whose activity ceases first when the temperature is lowered, namely, the developing egg. In this connection it will be

recalled that the egg of *Smynthurus* continues developing at a perceptible rate, down to 5°C. However, since mean monthly temperatures have been utilised, the lower temperature limit has been determined as 6·6°C. or 44°F., development below this temperature being so slow as to require several years for completion, even assuming that the very low temperatures experienced during the colder months, where such conditions obtain, are harmless. The northern and southern geographical limits of



Prediction of complete geographical range of existence and areas of economic significance of *Smynthurus viridis*.

existence of the insect are therefore determined by a line drawn through those points on the surface of the earth whose mean temperature, for the warmest month of the year, does not exceed 44 F. Rainfall never acts as a limiting factor in such areas. On the other hand, the southern and northern limits of existence in the northern and southern hemispheres, respectively, are determined sometimes by rainfall and sometimes by temperature, depending on whether the particular place has a mean monthly temperature exceeding 66 F. or a total monthly rainfall of less than 0·12 inches. In either instance the continued existence of *Smynthurus* is impossible, irrespective of the favourability of all other factors.

Once the necessary meteorological data had been obtained, the geographical limits of existence of the insect were relatively easy to determine, and have been charted in the outline map of the world presented herewith. The stippled areas indicate the regions of the world in which continued existence of *Smynthurus* is, theoretically at least, impossible, and it remains for others to prove by the discovery of the Collembolan living permanently in those areas that the writer's prediction is incorrect. There may be certain favourable areas in the semitropical parts of the world which support a meagre population in exceptionally favourable years, by influx from surrounding areas, but these have been excluded from the map, since the latter is intended to represent conditions which obtain on the average. In this connection, it must be emphasized that the limits of existence are by no means immutable, but oscillate about the mean limits indicated on the map, on account of continually fluctuating environmental factors. The large double circles, within the stippled regions, in Peru, Southern India, and Ceylon, indicate isolated areas which are climatically favourable to the insect on account of high altitude, and there may be similar isolated areas in the highlands of Abyssinia and Kenya, but meteorological records were not available.

8. Prediction of Areas of Economic Significance.

The next step in this bioclimatic study of *Smynthurus* was to determine the optimum conditions for existence of the insect. This is not so easy, since at best it is essentially a compromise between a variety of conflicting physiological requirements on the part of the organism concerned, for reasons already discussed in Part I of this paper, and hence the optimum natural environment is that which presents the most effective compromise to those conflicting requirements. The initial procedure consisted in determining what the writer has called the "critical points," these being the amount of rainfall and degree of temperature, any departure from which (in an upward direction for rainfall, and downward for temperature) did not evoke any further appreciable response on the part of the organism, as indicated by an increase in population, but from which a deviation in the opposite direction resulted in a profound reduction. Since the typical response of organisms to successive increments of a particular factor (in so far as its effect upon population increase is concerned) assumes the form of a sigmoid curve, it will be understood that the critical point is located at the crest of the curve beyond the mid-point of inflexion.

By referring to Graph 15 (*a*), in which the effect of factorial increment upon population increase is well illustrated, it will be observed that the critical point on the rainfall curve is 1·55 inches per 14-day interval. As regards temperature, the critical point is 57°F. Having thus ascertained the critical rainfall and temperature, respectively, it is relatively easy to fix the limits of these two environmental factors, such that *Smynthurus* may be expected to increase very rapidly and maintain a high population. The other rainfall limit would appear to be 6 inches a month, when adverse secondary factors come into operation; and the other temperature limit is 52 F., owing to the rapid slowing up of the growth rate at temperatures below this point, with consequent delay in the arrival of sexual maturity, one of the most important factors for the maintenance of a high population level in nature. The

reason for locating the critical points on the crest of the sigmoid curve beyond the mid-point of inflexion, and not where the curve reaches the asymptote, is that the latter would represent the theoretical maximum of the factor, which seldom exists under natural conditions; and further, their relation to the organic response of the insect is such that when those conditions obtain, *Smynthurus* is very favourably situated for the production and maintenance of a high population. Hence we are now in a position to state that from our knowledge of the dominating rôle of rainfall and temperature in the natural control of the insect in Europe, the *Smynthurus* population will attain to almost its maximum natural level in those areas where there is a rainfall of 3·1–6·0 inches a month, together with a mean monthly temperature ranging between 52·0° and 57·0 F., provided that there does not exist a significant biotic factor of control which is not present in the insect's original home. Further, from considerations relative to the economic status of the insect in Europe and Western Australia, the damage it causes to lucerne and clovers will be of economic significance whenever and wherever such conditions of temperature and rainfall obtain for two consecutive months. The non-conformance of the environment to any one of these climatic requirements offsets the favourability of the other, and thereby renders impossible the attainment of a population density sufficient to bring about damage of economic importance.

One further point concerning the climatology of *Smynthurus* remains to be considered, namely, the determination of those parts of the world in which it is not normally of economic significance, but may become so whenever the climate deviates from the mean in a direction favourable to the insect. This involves warmer conditions for those areas in which the normal mean monthly temperature is lower than 52 F., cooler conditions for those areas in which it is higher than 57°F., and a heavier rainfall for those areas in which the monthly total is normally less than 3·1 inches. To determine such areas with mathematical accuracy would involve fairly advanced statistical treatment together with the compounding of probabilities, and it is not intended to pursue this avenue of approach meantime. All that is intended, for the present, is to indicate those areas in which *Smynthurus* may become of economic significance occasionally, irrespective of the actual probability of occurrence. In general, such areas are characterised by a total monthly rainfall of not less than 2·5 inches, combined with a mean monthly temperature within the range 51°–58°F., exclusive of those areas which conformed to both the temperature and rainfall requirements of the optimum environment. As in the latter instance, the climatic conditions indicated must obtain for two consecutive months.

The areas of occasional economic significance have been represented in the outline map of the world by means of a solid circle, whereas the areas in which the pest is normally of economic significance (*i.e.*, almost every year) have been represented by means of a double circle. It will be observed from the map that the circles are grouped with a fair degree of precision into three main regions, namely, (*a*) the western, southern, and eastern portions of Australia and the whole of New Zealand; (*b*) the northern and southern parts of Argentina and Uruguay, respectively, and the coastal regions of Chile; (*c*) the countries immediately surrounding the Mediterranean Sea and the north-western parts of the British Isles. However, *Smynthurus* does not flourish abundantly in all these favourable areas at the same time or even the same season of the year, being found in greatest numbers in Western Australia, for example, from May to August; in countries bordering the Mediterranean, from February to April; and in Britain during June and late August, the intervening period being too hot and dry. Thus it finds conditions most favourable in Australia during the winter season, during spring in those regions bordering the Mediterranean, and during early summer and early autumn in Britain.

In order to demonstrate that the theoretically possible distribution in no way conflicts with the actual distribution, so far as known from all available records, and

also that there are several highly favourable areas, climatically at least, to which *Smynthurus* has not yet penetrated, a list of the meteorological stations recorded in the outline map of the world, together with the known distribution of the insect, by countries, has been prepared and presented in Table XVI.

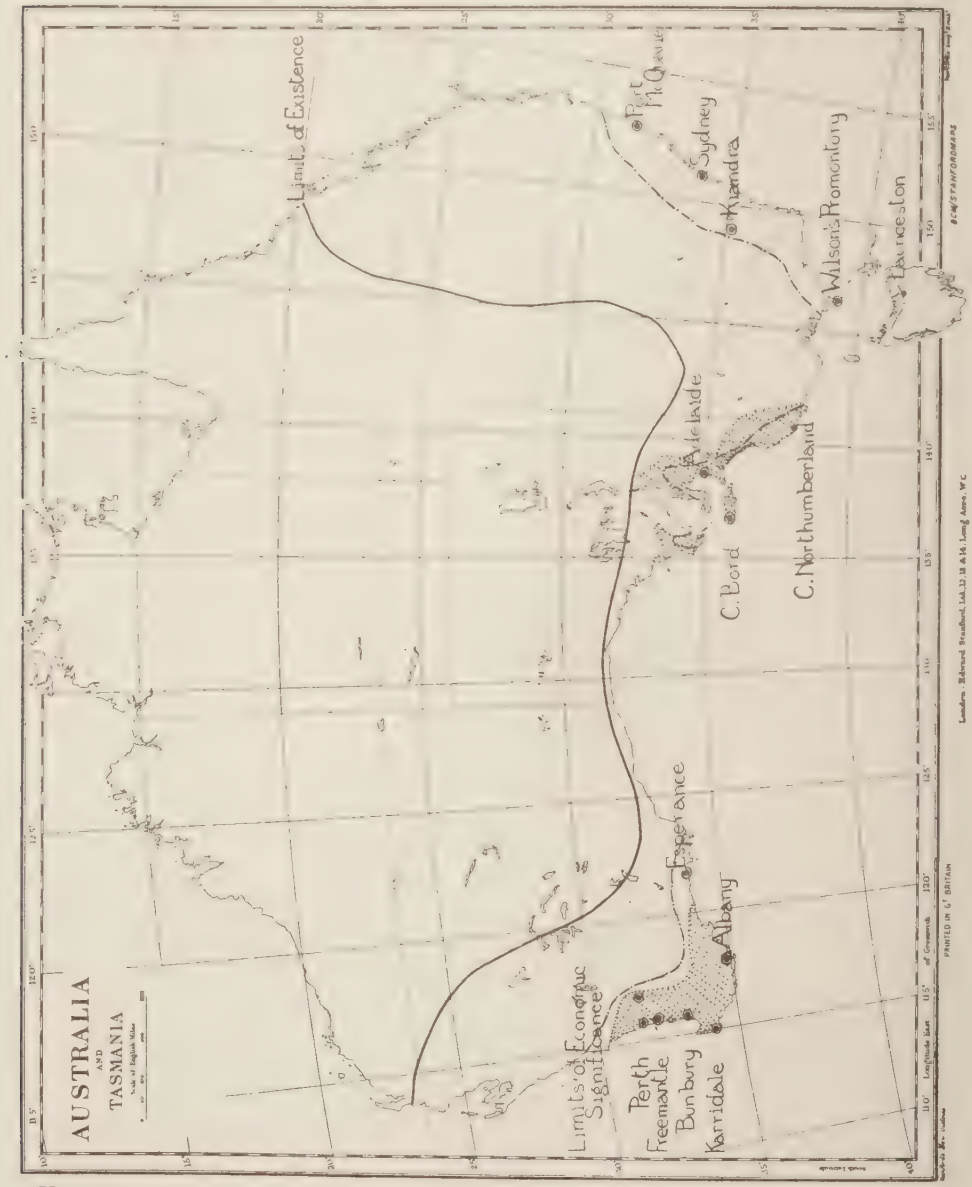
TABLE XVI.

Theoretical distribution of *Smynthurus viridis* according to climatic requirements, into—(1) Favourable and (2) Highly Favourable Areas.		Known geographical distribution of *Smynthurus viridis* (by countries).
(1)	(2)	(3)
North America: Valdez, Juneau, Eureka, San Francisco, Father Pt., Hatteras, Mobile, Charleston.	*North America*: Kodiak, Sitka, Barkerville, San Louis Obispo, Galveston, New Orleans, S. W. Point.	*Europe*: Russia, Finland, Germany, France, Switzerland, Italy, Rumania, Hungary, Bulgaria, Sweden, Denmark, British Isles, Spitzbergen.
South America: Bogota, La Paz, Buenos Aires, Pt. Monte.	*South America*: Quito, Valparaiso, Ancut, Valdivia, Porto Alegre, Monte Video, Rio Grande.	*Africa*: Algeria, Morocco.
Europe: Bodó, Trondjhem, Bergen, Deerness, Wick, Nairn, Aberdeen, Armagh, Killarney, Malin Head, Bilbao, Santiago, Andermatt, Belluno, Genoa, Leghorn, Rome, Naples, Lesina, Ragusa, Athens, Corfu.	*Europe*: Christiansund, Glencarron, Fort William, Cally, Douglas, Buxton, Markree, Oporto, Lisbon, Coimbra, Gibraltar.	*Asia Minor*: Iraq.
Asia Minor: Beirut, Gaza.	*Asia Minor*: Haifa.	*Australia*: Western Australia, South Australia, Tasmania.
Africa: Safa, Tripoli.	*Africa*: Oran, Algiers, La Calle, Cape Town.	*South America*: Argentina.
Australia: Cape Northumberland.	*Australia*: Perth, Banbury, York, Albany, Karridale, Esperance, Pt. McQuarie, Sydney, Kiandra, C. Borda.	
Small Islands: parts of Cyprus, Azores, Canary Is., Iceland, and Tasmania.	*New Zealand*: Auckland, New Plymouth, Wellington, Hokitika, Dunedin, Invercargill.	
	Small Islands: Cyprus, Malta, Sicily, Canaries, Balearics, Azores, Valencia Is.	

From the latter it is evident that there are several countries to which *Smynthurus* is potentially a serious economic menace, the most important of these being New Zealand, the south-west corner of Cape Province, Natal, Chile, New South Wales, and the United States of America (northern California, South Carolina, southern Alabama, and Georgia). The question of soil type has not been taken into consideration in the prediction of the favourable areas, because on the average (the condition for which the theoretical distribution map has been constructed) the controlling effect of soil type is of very minor significance in comparison with climate. However, in certain instances where the hydrogen ion concentration lies outside the range 5·5 to 7·0 on the pH scale or the soil is of a remarkably porous nature, our predictions as to the probable abundance of the insect cannot be expected and are not intended to hold good. In such circumstances, or if it is intended to predict the average abundance of *Smynthurus* in a relatively small area, soil type enters as an additional complicating factor which must receive due consideration in our calculations. Hence until the soil chemists have prepared accurate survey maps, the prediction of the geographical distribution and abundance of many terrestrial arthropods will be seriously handicapped.

9. Known Distribution and Areas of possible Colonisation in Australia.

As the economic significance of *Smynthurus*, at the present time, is of greatest moment in Australia, it has been attempted to portray the distribution of the insect in that part of the world with somewhat greater detail than was done for the world as a



Known distribution and areas of possible colonisation in Australia of *Smynthurus viridis*.

whole. The accompanying map illustrates, by means of stippling, its known distribution in Australia and Tasmania, while the broken line indicates the approximate limits of economic significance, and the solid line, the limits of existence.

The distribution in South Australia is taken from Dr. Holdaway's paper, and for the approximate distribution in Western Australia the writer is indebted to Mr. L. J. Newman. For the accuracy or inaccuracy of the areas delimited by the broken and the solid lines the writer is entirely responsible. It will be observed that in South Australia, from which it was first reported in that continent, *Smynthurus* has spread beyond the limits of economic significance, whereas in Western Australia, it has not yet reached those limits. In neither instance has the insect attained to the limits of existence, although it is much nearer to them in South than Western Australia, and consequently the rate of dispersion inwards will be much more rapid in the latter than in the former. The map also indicates that there is a large tract of country in New South Wales and southern Victoria from which the insect has not yet been recorded, but to which, in the event of its introduction, it would undoubtedly prove to be a serious economic problem. Also, there exists a fairly large band of territory in the North and Western parts of Tasmania which is highly favourable for the production and maintenance of a large *Smynthurus* population, although the insect has been introduced into the island only within the last few years, and therefore has not yet had time to demonstrate its full potentialities as regards numerical increase.

The great value of a bioclimatic study lies in the fact that it renders possible the prediction of animal abundance and distribution, both seasonal and geographical. For some unknown reason, properly conducted scientific studies of this type have been comparatively neglected. Within the last few years, however, the subject has been receiving increasing attention, and the writer is convinced that, as a field of scientific endeavour, bioclimatics offers results of great promise from the viewpoints of both economic and purely academic research; and further, that in future the results of such studies will be one of the most important tools employed by the economic biologist.

III. Applied Control and Remedial Measures.

1. Utilisation of Insect Predators.

In considering the possible applied controls and remedial measures which may be adopted in any attempts to maintain the population of *Smynthurus* below the level of economic significance, it will be remembered that a list of predators was given in Part I (p. 125), in order of efficiency, based entirely on laboratory feeding tests. This (as then stated) was of little value as an aid to the final choice of predators with a view to their utilisation as biological agents of control, because it left out of consideration such factors as density of predator population, seasonal abundance, ecological relationship between prey and predator, and the feasibility of collecting or rearing an adequate number of them. However, since each species was briefly analysed from an ecological viewpoint in Part I, and the action *en masse* of the insect and arachnid predators has been discussed (pp. 118–124), we are now in a position to make an analysis of the feasibility of biological control as regards this species, bearing in mind always that such attempts are intended to be economically justifiable and not merely interesting biological experiments. This immediately rules out of consideration all but those bracketed as "good predators," and even this list must be subjected to some culling.

Number one on the list, namely, *Forficula auricularia*, L., is obviously out of the question as a possible biological agent of control, since it has proved itself a serious pest on introduction into countries outside Europe, particularly in the Pacific North-West of America and in New Zealand. The next species, *Paederus littoralis*, Grav., is in almost every respect suitable for introduction to Australia, as it is found in considerable abundance in nature, is easy to maintain alive for long periods under laboratory conditions, and occupies a similar habitat to *Smynthurus*. The writer succeeded in obtaining eggs of this Staphylinid in the laboratory, from which larvae

eventually emerged. However, another species belonging to the genus *Paederus*, namely, *P. cingulatus*, Macl., has been recorded as an enemy of *Smynthurus viridis* in South Australia by Holdaway, so that the chances of the European species bringing about significant control, where the native one is apparently unable to do so, are very small indeed. In fact *P. littoralis* may already be present in the Australian environment, although it has not been recorded, and in this connection the writer takes the opportunity of stating that one of the essential preliminaries to the introduction of biological agents of control is a survey of the main biotic factors already present in the country of introduction, before launching out on a large scale shipment of parasites or predators.

The third species on the list is the common Ladybird (*Coccinella septempunctata*, L.), well known as a devourer of Aphids and with a wide geographical distribution, having been recorded from almost every country in Europe, as well as from North Africa, Siberia, and India. However, despite great climatic adaptability, together with a great catholicity of taste (see Part I), it is highly questionable whether the introduction of this species into Australia would have any significant effect on the *Smynthurus* population, as the Collembolan is not its primary source of food but apparently acts as a stop-gap in times of Aphid scarcity, or when *Smynthurus* is unusually abundant and thus more readily obtainable. Besides, it was evident from an analysis of the field data that the effect of all Coccinellids on the *Smynthurus* population in England and the South of France was negligible, except in the above circumstances. We are thus left with only two good insect predators as possibilities for economic utilisation, these being *Lathrobium brunnipes*, F., and *Cyrtosus cyanipennis*, Er. A small preliminary introduction of both species to South and Western Australia would appear to be a rational, economically justifiable procedure, and for the following reasons. The former is a member of the same subfamily (PAEDERINAE) and the same tribe (PAEDERINI) as the two good predators of *Smynthurus*, *Paederus cingulatus* and *P. littoralis*; moreover, it prefers damp situations, as *Smynthurus* does, and since it is found commonly throughout England in moss and vegetable debris, at the roots of grasses, etc., it could be collected without much difficulty in sufficient numbers for such a shipment. The Melyrid, *Cyrtosus cyanipennis*, Er., flourishes under the climatic conditions of the Mediterranean littoral, which are somewhat similar to those of Western Australia, where *Smynthurus* causes such serious damage. Both species proved themselves to be voracious devourers of *Smynthurus* (see Part I).

2. Utilisation of Arachnid Predators.

Coming to the spider predators it will be recalled that the field data indicated a closer correlation between the *Smynthurus* population and the spider population than any other constituent of the biotic environment. From laboratory feeding tests and ecological relationships, it was also shown that members of the families THOMISIDAE, or Crab-Spiders, and LINYPHIIDAE, or Dwarf Spiders, were amongst the most efficient *Smynthurus* predators. However, having examined quantitatively the rôle of spiders in checking *Smynthurus* in nature, we can now proceed further and state that of all the natural biotic agents of control spiders appear to exert a greater effect than any other biotic factor of control. Hence the possibility of their economic utilisation demands careful consideration.

The most important species, in this connection, are (1) *Tibellus oblongus*, Wal.; (2) *Xysticus* sp. (*cristatus* ?); (3) *Philodromus* sp (*dispar* ?); (4) *Lephthyphantes zimmermannii*, Bertk.; (5) *Erigone atra*, Blkw., and *E. dentipalpis*, Wid.; and (6) *Pachygnatha degeerii*, Sund. The chief points of interest concerning these spiders have already received attention in Part I, so that it will be unnecessary to repeat them here. The first three species are all Thomisids and quite common throughout England; indeed the Crab Spiders were the most numerous of the *Smynthurus* predators taken in the field sweepings. Their collection in sufficient numbers for shipment would not

present, therefore, a very serious problem, the months of greatest abundance being August, September, and October. As these species possess considerable climatic adaptability, being found over a wide range of territory, the question of survival in sufficient numbers to exert a controlling influence is of little moment, so far as their introduction to Western Australia is concerned. The Linyphiid species (4 and 5) present greater difficulties in regard to prediction of their survival under the climatic conditions obtaining in Australia. Hull states that the family is the predominant one in temperate and arctic regions. "Even within the limits of Great Britain," he says, "the proportion of spiders belonging to the family Linyphiidae, increases as one proceeds northwards." Also, it is known that very few species have been recorded from the Australian continent, the reason for this being probably climatic, as the species are relatively small, and judging from laboratory observations, somewhat susceptible to low humidities. However, since they make up in numbers for what they lack in size, and they undoubtedly exert some controlling influence on the *Smynthurus* population in Britain, a small preliminary shipment to determine their survival capacity in the Western Australian environment would appear to be an economically justifiable procedure. The species mature in early summer and gradually disappear from the middle of May onwards, the tiny young appearing in numbers by September, and becoming very abundant in October and November. During those months, the collection of these spiders in adequate numbers for shipment would be a relatively simple matter.

The idea of utilising spiders in the biological control of insects may be regarded by some as being rather unorthodox, to say the least, owing in large measure to the prevailing exaggerated opinion concerning the rôle of entomophagous parasites in the control of natural populations. A word in support of the arachnids may, therefore, not be out of place. Regarding the part played by entomophagous parasites in nature, several valuable papers by Dr. W. R. Thompson, published within the last few years, have done much to dispel many illusions and to place the subject of biological control in its proper perspective. In one of these, Dr. Thompson calls attention to the almost universally under-estimated value attached to insect predators, on account of their supposedly interior specificity, and states that they "are at least relatively restricted in their choice of food, and since this is the most we can say of parasitic insects, of which many are extremely polyphagous, the average predator cannot on the score of specificity be considered as markedly interior to the average parasite." The same argument as to specificity is invariably adduced against the employment of arachnid predators, and the writer believes it to be equally unjustified. Several famous naturalists have long ago remarked on the voracity of many spiders and their important rôle in the economy of nature. In the introduction to his monograph on the "Spiders of Great Britain and Ireland," Blackwall says, "By contributing to check the too rapid multiplication of insects, from which they chiefly derive their sustenance, spiders perform an important part in the economy of nature." Again, the well known American arachnologist, McCook, in his voluminous work on the "American Spiders and their Spinning Work," says, "The number of insects which a healthy spider is able to devour during a day, without apparent inconvenience, has often been a great surprise to me." Perhaps the best known arachnologist of all, the Rev. O. Pickard-Cambridge, in his introduction to the "Spiders of Dorset," goes so far as to state that, "The spider is doubtless nature's chief check against the undue increase of insects. Despised Arachne is entitled by her services to occupy the chief place among invertebrate philanthropists." This seems to be overstating the case, but at least serves to draw attention to a group of Arthropods whose predatory activities appear to have been underestimated in recent researches (mostly by entomologists) into the intricate phenomena associated with natural control.

3. Mechanical and Cultural Methods of Control.

As the purpose of the present paper is to provide a rational scientific basis for the

choice and putting into operation of control measures rather than with the actual measures themselves (other than biological), it is not intended to discuss in any detail the subjects indicated in this sub-heading. The details of such artificial controls vary to such an extent, depending upon the soil type, rotations adopted, local agricultural practices, etc., that the writer believes that such an attempt would be essentially futile, and should be left to the judgment of those immediately concerned with the supervision of control measures in their particular locality. However, there are certain obvious measures which immediately suggest themselves as a result of this scientific analysis of the situation, and which may serve as guides to those whose duty it is to elaborate the necessary details before putting such artificial controls into effective operation.

Since soil moisture plays an all-important part in the propagation of the species, anything which tends to reduce the moisture content of the surface layers of soil will help to minimise infestation. This can, of course, be best obtained by mulching the top two inches of soil. Alternately harrowing and rolling the soil surface would not only help the production of a fine tilth, but would result in the crushing of many eggs, nymphs, and adults. The introduction of a bare fallow into the rotation, where this is not the custom, would expedite these measures, and render possible deep ploughing, with a view to burying all stages by a complete inversion of the furrow. Bare fallowing is also advantageous from the point of view of starving the insect, provided that it is accompanied by the above mechanical measures, and all weeds are eliminated.

The application of lime to the soil to render it more alkaline has been suggested by Holdaway, and this would appear to be a feasible remedial measure where the cost is not too great. Once the pH value, or lime requirement, had been determined, the economics of the situation may be gauged, but in any case the soil pH value should be raised to not less than 7·0, otherwise it is doubtful whether the increased control would repay the labour involved. The question of chemical control is outside the province of this paper and will therefore not be considered, except to state that from our knowledge of the effects of environmental factors upon *Smynthurus*, lime compounds have certain obvious advantages on account of their adverse alkalinity effect and their capacity to absorb moisture.

From general observations in England and Scotland it was apparent that man's disturbance of the natural environment in the husbandry of stock and crop had very different effects upon the *Smynthurus* population, sometimes rendering conditions more favourable and sometimes more adverse, depending upon the prevailing agricultural practice. Intensive grazing, for example, was found to exert a profound influence in lowering the level of the *Smynthurus* population, as will be seen on referring to Graph 16. This field (namely, Field C) is adjacent to Field B, and is almost identical with the latter as regards texture, structure, and reaction of the soil type, insect and arachnid fauna, cultural treatment, etc., but differs from it in that cattle and horses are grazed therein for the greater part of the year. The population density is markedly less than in B. One is therefore forced to the conclusion that intensive grazing exerts a powerful check upon the increase in numbers of *Smynthurus*, by means of the trampling action of the stock in crushing eggs, nymphs, and adults, while many must be swallowed with the herbage. Heavy stocking of pastures with cattle and sheep should therefore be practised wherever the agricultural economics of the situation render this feasible.

IV. General Conclusions.

As a result of this investigation, originally prompted by economic motives, there have been developed several conceptions of general biological and ecological significance from a purely scientific standpoint. In the introduction it was stated that the

intention throughout the paper was not simply accumulation of data but also interpretation of the latter, in so far as this was scientifically justifiable. This primary objective has been continually borne in mind. Moreover, throughout the course of the investigation the writer has stressed the fundamental principles involved and the logical method of procedure, with a view to placing the entire study on a sound scientific basis. In reading through many of the present-day "research papers" such considerations are apparently regarded as superfluous, but are none the less necessary, especially in a young science like ecology, which has not even attained to adolescence, and consequently still requires much guidance if a normally healthy adult is to be produced. On account of the complex nature of the investigation, its presentation has by no means been an easy task, but it is hoped that so far as possible each of the many components has been placed in proper perspective and that the various facts have been presented as a balanced and comprehensive unity.

1. Economic Considerations.

As regards the economic aspect, a mass of evidence has been produced to show that the major factor, or combination of factors, responsible for the abnormally high *Smynthurus* population in Western and South Australia are abnormally favourable conditions of rainfall and temperature—much more so than those obtaining in the original home of the insect—not only in regard to actual climatic conditions but also in that they prevail uninterruptedly for a longer period and so allow the rate of increase to gather momentum. Since populations tend to increase in a geometrical progression wherever environmental conditions are favourable, it is evident that in such circumstances a doubling of the rate of increase, or even one more generation, may make all the difference between a population density of no economic significance and one sufficient to produce a "plague."

The maximum density of *Smynthurus* was obtained on 26th June in Field B (the most favourable environment for the species encountered in the investigation) and since it was found by trial that the numbers obtained by the stroke method represent approximately 75 per cent. of the actual population, it follows that the true number per stroke was 104, making a true density of almost 14 per square foot. The writer is unaware of the density obtaining in Australia, but judging from climatic considerations alone it must be considerably higher than in England, and a density of twice this amount would certainly mean that *Smynthurus* assumed the economic status of a serious pest in this country, in so far as damage to clover pastures is concerned.

The problem of controlling the pest by biological methods has been treated in considerable detail and serves to demonstrate that a dispassionate analysis of the facts relative to the environmental controlling complex is an essential preliminary to placing the biological method of control on a economic and scientific basis. This involves not merely a consideration of biotic factors of control but the whole complex of biotic and physical factors, since the latter have a profound influence on parasite, predator, and host, resulting in a maze of often unsuspected inter-relationships. The physical environmental factors undoubtedly assume the major rôle in the natural control of insect populations, but this does not mean that the biotic factors are on that account negligible and can be immediately disposed of. On the contrary, the assessment of their true significance as natural agents of control is thereby rendered more difficult, and requires an investigator with a broad academic background and penetrative intelligence, if the true rôle of biotic factors in each particular instance is to be analysed, and the chances of success in their economic utilisation is to be gauged with a reasonable measure of certainty. Pending the analysis of the environmental complex, inexpensive tentative measures should, of course, be put into operation.

As regards artificial remedial measures (other than chemical), the investigation has shown that these must centre round a judicious manipulation of the microclimate, with the object (in this instance) of thereby lowering the humidity and raising

the temperature to an extent compatible with the prevailing type of agriculture; also, the nature of the pest renders feasible direct mechanical treatment with a view to crushing eggs, nymphs, and adults, the latter being arranged to fit in, as far as possible, with the routine cultural measures in the husbandry of stock and crop, in order to minimise expense.

2. Ecological Considerations.

Coming to the more direct ecological relationships, especially the bioclimatic aspect, the writer realises the danger of entering the realms of prophecy, but at the same time believes that the prediction of abundance, outbreaks, and distribution of insect populations, is full of promise for the future, and will yet prove to be the most efficient weapon in the hands of the economic entomologist. To draw a parallel from medicine, a stage has been attained in the science in which it can be said that prophylactic measures are in every respect superior to therapeutic treatment. The rapidity of the advance in this direction will depend to some extent upon the meteorologist, but as the latter scientist has shown his willingness to co-operate with the biologist, and in view of the advances being made along the lines of long range weather forecasts, it seems reasonable to conclude that bioclimatics have every prospect of providing a fruitful field of scientific endeavour and should yield results of great interest and value in the near future.

The analysis of the environmental controlling complex of *Smynthurus* affords a good concrete illustration of how such complexes continually vary in their composition and structure, both spacially and chronologically; the variation, although continuous, is by no means uniform, and the fluctuations, although often sudden, take place with some degree of regularity when viewed over a period of time, thereby rendering prediction of the organic response a statistically feasible proposition.

3. Evolutionary Considerations.

Critically planned laboratory experiments bearing upon the "field physiology" of the insect have served to demonstrate that the living organism is by no means the beautifully co-ordinated and harmonious physiological unit that it is so often represented to be. Doubtless this fact is more pronounced in *Smynthurus*, on account of its lowly position in the evolutionary scale, than in many other more highly evolved organisms in which the various co-ordinating and regulating mechanisms are better developed; *e.g.*, hormones are known to be deficient in the invertebrates. Nevertheless, although we may *a priori* expect to find a greater degree of harmony between the various physiological systems of the individual as we progress up the evolutionary scale, it seems that in many instances this diverse physiological ensemble sets a severe handicap upon environmental adaptation. Further, the deeper one delves into the quantitative study of organism and environment the more critical one becomes concerning their harmonious relationships. What actually appears to take place in nature is that the organism is continually mustering its forces to the attack of a hostile environment, which it proceeds to conquer with varying degrees of success, by occupying situations in which it is less prone to adverse agencies, by the elaboration of mechanisms which buffer external changes of an unfavourable character, and in the highest stages, by the creation of an immediate environment of its own, which thereby renders the organism to some extent independent of the adverse circumstances presented by the external environment. The writer does not mean to imply that actual modification of morphological structure and physiological function in response to environmental changes no longer occurs as an integral evolutionary function, but simply that it does not and never has proceeded to the extent often imagined; those so-called "hand-to-glove" adaptations, in particular, being mere fictions of the imagination resulting from over prolific biological philosophising.

As a quantitative study in the modern outgrowth of the older science of natural history, known as ecology, it is hoped that the present investigation will contribute towards the consolidation and reinforcement of the latter as the fundamental basis of all applied biology.

V. Acknowledgments.

The writer is indebted to many of his associates in the laboratory and elsewhere for helpful advice and criticism at various times throughout the progress of the investigation. The first of those is Dr. W. R. Thompson, for laboratory facilities provided, and for the keen interest shown throughout the progress of the work. To Sir Guy A. K. Marshall the writer is indebted for the identification, through the Imperial Institute of Entomology, of the various insect predators. The writer also wishes to extend his grateful thanks to Dr. A. D. Imms for permission to carry out the investigations made at Rothamsted; to Dr. P. A. Buxton, for advice in connection with the humidity experiments; to Mr. W. S. Bristowe, for kindly identifying the spider predators; and to Messrs. Kozlovsky and de Rippas for the collections from France. Thanks are also due to Messrs. Edward Stanford Ltd. for permission to reproduce the outline maps on pp. 178, 182. Finally, the writer acknowledges with appreciation the labours of Mr. R. C. Jeffery in connection with the manuscript and for re-drawing the original graphs much to their improvement.

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OVIPOSITION STIMULI OF THE BURR-SEED FLY, *EUARESTA AEQUALIS*, LOEW (DIPT. TRYPETIDAE).

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(Plate VIII.)

A Section of the Division of Economic Entomology of the Commonwealth Council for Scientific and Industrial Research is devoted to the attempted control of noxious weeds by means of their insect enemies.

One of the weeds being studied is a plant known locally as Noogoora Burr (*Xanthium pungens*), which is a serious pest in some of the sheep districts of Queensland : the ripe burrs stick to the fleece and so reduce the value of the wool.

As North America is considered by most authorities to be the original home of the Xanthiums, Dr. R. J. Tillyard, Chief of the Division of Economic Entomology, decided that the search for insects should begin there. Mr. S. G. Kelly, a graduate of the Kansas State Agricultural College, is working for the Council, and has already discovered a number of insects which attack *Xanthium* spp. exclusively. The first insect studied was a seed fly (*Euaresta aequalis*, Lw.). When it had been found that, in the opinion of the investigator, this species would not be likely to attack economic plants, burrs containing larvae were despatched to Australia, where they were received into quarantine insectaries for further testing before liberation. This fly has never been recorded as infesting any plant except species of *Xanthium*.

The fly is a typical Trypetid, but the females have unusually large ovipositors, adapted for laying eggs inside the hard burr capsule, which is protected by hooked spines. The colour of the fly is an even lemon-yellow, the eyes brilliant green, and the wings have smoky grey maculations, which are clearly shown in the accompanying photographs (Plate viii).

The length of the body is about 6 mm., and the extended ovipositor protrudes 2·1 mm. beyond the body as a strongly chitinised brown tapering tube (fig. 1). The dart-shaped strongly-chitinised tip has to bore through the tough outer coat of the burr, and the egg is passed inside the seed, where the young larva develops.

It is clear that in the case of a seed fly the only tests of value in establishing the fact that the fly is innocuous to economic plants are oviposition tests. Accordingly after the adults had emerged from the burrs sent from North America and the females had reached maturity, definite oviposition tests were begun.

The first test was designed to show whether or not the flies would oviposit in captivity on their normal food-plant. This they did without hesitation.

A series of selected fruits of economic importance, in the fresh green state, were then exposed to the females, both individually in cages and in bulk in a larger enclosure, but no oviposition or attempted oviposition was observed. When they were given a small branch of *Xanthium pungens*, however, oviposition began immediately on the burrs.

When liberated in an insectary containing a number of different plants, including some *Xanthium pungens*, the flies quickly found their natural food-plant and stayed there. This finding of the food-plant was obviously a chemotactic reaction to the odour of *Xanthium*.

Green capsules of *Datura stramonium* were placed with the flies in a cage, and it was observed that when gravid females wandered over the spiky surface they became excited and tried unsuccessfully to penetrate the hard coat with the ovipositor. The absence of hooks on the tips of the spines appeared to hamper the females in their attempts to oviposit, as they could get no grip with their feet to act as a purchase in driving the ovipositor through the tough capsule. They also reacted in a similar way when wandering over the spiny surface of the bracts behind a sunflower head.

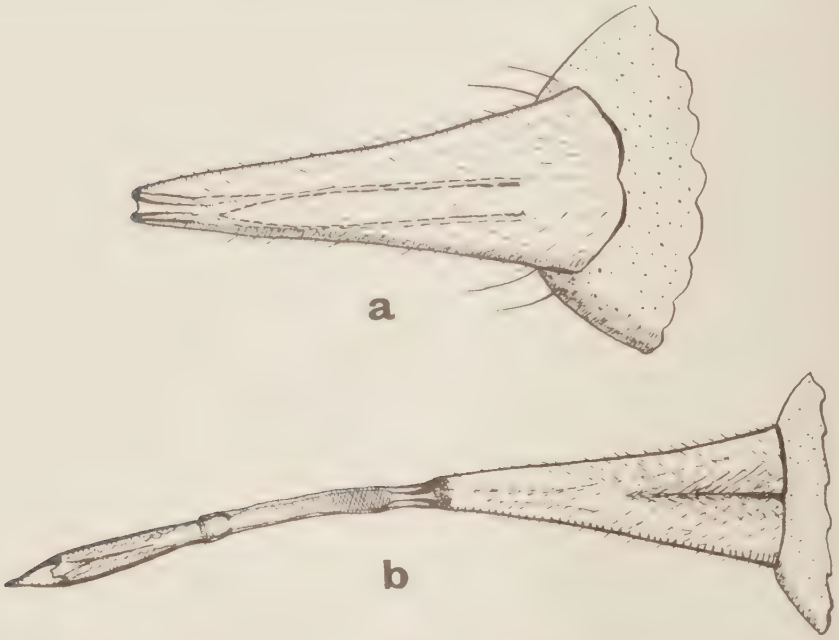


Fig. 1. *Euaresta aequalis*, Loew: *a*, ovipositor as it appears at rest (× about 33); *b*, ovipositor extruded to its full length, when it measures about 5 mm. (× 24).

It was considered that if it could be shown that oviposition was definitely connected with a certain set of successive stimuli, more point could be given to the argument that the flies were harmless to economic crops than was possible with the usual routine tests. Accordingly, further investigation of these stimuli was carried out as follows :—

Green burrs of *Xanthium pungens* were stripped bare of the spines covering their surfaces and placed with gravid females in a cage. The flies showed excitement and walked rapidly over them, but did not attempt to oviposit.

Pieces of rubber were then cut to the shape of burr capsules and studded with small entomological pins, hooked at the ends like the hooked spines of *Xanthium*. When these were placed with the flies they took little notice of them, but when actually placed *on* them they showed an interesting reaction. On moving over the spiny surface the gravid females showed excitement, and dipping their ovipositors commenced to drive them into the " burrs " in an effort to oviposit.

There was a considerable variation in the reactions of females to these artificial burrs. Some females could not be induced to attempt oviposition on them, although they would do so readily on their own food-plant. Others were somewhat hesitant, and clearly were not enthusiastic about this artificial burr as a place in which

to oviposit. The majority, however, when fully mature, and particularly when they had been mature for some time and had had no opportunity to oviposit, took to the artificial burr readily and drove into it energetically with the ovipositor.

The accompanying photographs show the artificial burrs with a female in the act of ovipositing, and also the natural burrs with a female ovipositing (Plate viii).

When a flat surface of cork was studded with hooked pins, females moving over it showed little interest. One female only was seen to dip the ovipositor as if to lay. When a small piece cut from a green burr was placed amongst the pins, the females jostled each other to get near it to suck the juices (in spite of being plentifully supplied with sweetened water and cubes of sugar), but did not attempt to oviposit. The shape of the burr may then have something to do with the stimuli concerned with oviposition.

To sum up :—

(*a*) Females and males reacted to the odours emanating from their food-plant by flying to the plants and settling there.

(*b*) Females, when mature, would react to certain spiny surfaces (other than the burrs of their natural host), such as *Datura* capsules, by attempting oviposition.

(*c*) Females would not attempt oviposition on the burrs of their natural host if the spines were removed from them.

(*d*) Females when fully mature would react to artificial burrs by attempting to oviposit on them.

(*e*) Females could not be induced to oviposit freely on a flat surface, even when it was studded with hooked spines.

It would appear that there are probably four successive stimuli necessary for oviposition in the mature seed fly (*Euaresta aequalis*), viz.:—

(1) The characteristic odour of its host, which enables the fly to find and recognise it.

(2) A body (fruit) of a size and shape of the same order of magnitude as the " cockle " burrs.

(3) A spiny surface which gives the immediate local stimulus to dip the ovipositor, and penetrate the burr ; and hooks on the spines to give the flies a good foothold for purchase in penetrating the capsule.

(4) (Presumably) A capsule of a texture which will allow the ovipositor to penetrate, and an egg to be passed down into the seed.

The photographs of the fly in the act of ovipositing were taken in the laboratory by flashlight. The camera used was the property of, and invention of Dr. A. J. Nicholson. A full description of this camera has been given in the Bulletin of Entomological Research, xxii, p. 308.

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Thanks are due to Dr. R. J. Tillyard, Chief of the Division, for helpful suggestions in the preparation of the manuscript, and to Dr. A. J. Nicholson for the use of his specially adapted camera.



Fig. 1

Euaresta aequalis, ovipositing on cluster of burrs of *Xanthium pungens*. (× 1·6)



Fig. 2.



Fig. 3.

Euaresta aequalis, ovipositing on artificial burrs. (× 1·6)

OBSERVATIONS ON *MELAMPHAUS FABER*, F. (HEM., PYRRHOCORIDAE) AND DESCRIPTIONS OF EARLY STAGES.

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Early in the month of January 1931 a large swarm of the Pyrrhocorid bug, *Melamphaus faber*, F., invaded trees of *Hydnocarpus anthelmintica*, Pierre, and *H. wightiana*, Blume, at the Government Experimental Plantation, Serdang, Selangor, Federated Malay States.

The insects were first noticed on 7th January, having apparently migrated from the jungle, the border of which is from one-half to three-quarters of a mile away, and arrived *en masse* on the *Hydnocarpus* trees.

Their sudden appearance can be accounted for only in this way, it would seem, since an insect so conspicuous in both its larval and adult stages, as is *M. faber*, would hardly have gone through a complete life-cycle and have escaped the notice of the collector of fallen ripe fruits who carries out this task daily. No alternative food-plant has yet been discovered.

A marked preference was shown by *M. faber* for the fruits of *H. anthelmintica*. The probable reason for this is that the outer rind of the fruit of this species is only 2 mm. thick and much less woody than that of *H. wightiana* and consequently less resistant to the stylets of the bug.

In the early days of the infestation large numbers of the insects were to be seen congregated in fairly compact groups in the main forks of the *Hydnocarpus* trees, when the sun was unobscured by clouds. A few isolated individuals were noticed feeding on exposed fruits, but the majority were resting in the most shady parts of the trees. The oil extracted from the nuts contained in the fruits of these trees is used in the treatment of leprosy. It is consequently of considerable importance that any reduction in the yield of such a valuable crop through the agency of insect pests should be prevented so far as possible.

Investigations were therefore initiated with a view to confirming whether premature fruit fall (which was above normal at the time of the infestation by *M. faber*) was caused by some mechanical injury inflicted by its piercing and sucking mouth-parts or by a fungous disease of which the bug might be a vector. In order to obtain information on this point, sound fruits were selected and several adult *M. faber* were enclosed in a gauze sleeve around them. Three weeks later the fruits were examined. Outwardly they exhibited no marked signs of injury, although some small greyish spots were present which might have been caused by the stylets of the bugs.

Other fruits in which *M. faber* was feeding were selected and brought to the laboratory, where they were enclosed in jars covered with gauze. From these fruits, both Nitidulid beetles (*Carpophilus* sp.) and Drosophilid flies emerged, which would lead one to suppose that *M. faber* is indirectly responsible for premature fruit fall, since by injuring the outer rind of the fruits it affords ingress to the beetles and suitable spots for oviposition for the flies, the larvae of which by further injuring the fruits cause decomposition. The adults and larvae of *M. faber* are very active and are disturbed by the slightest movements of the observer, endeavouring to conceal themselves by running round to the opposite side of the tree-trunk or fruit on which they happen to be.

When handled they secrete copiously a colourless and very objectionable fluid, which, unlike the fluid secreted by many other bugs, does not leave a stain after evaporating. The smell of this fluid does not remind the writer of any familiar odour, but a suggestion was put forward by Dr. T. A. Buckley, Chemist of the Forest Department, Straits Settlements and Federated Malay States, to whom some of these insects were submitted, that it resembled phenyl-acet-aldehyde.

It may be mentioned here that the smell of the immature nuts of *H. anthelmintica* resembles very closely that of stale raw meat.

When feeding on the fruit the insects pierce the hard outer covering and insert their stylets to their full length in order to reach the nuts inside. When the stylets have been forced into the fruit to about a third of their length, the labium is bent, the second and third segments forming a right angle more or less, but when they have been thrust in to their entire length the labium falls back into the position it assumes when the insect is not feeding.

Before beginning to feed *M. faber* explores the surface of the fruit or leaf-stalk with the tips of its antennae and rostrum, and after feeding cleans its stylets by drawing them through the tarsi of the forelegs, which it holds close together.

At the time when *M. faber* was first observed, a few copulating pairs were to be seen. A week later, however, only comparatively few were not copulating. When desiring to copulate the male sometimes climbs on the back of the female, and having effected the requisite connection, moves round either to the right or left until he faces in the opposite direction to the female. On one occasion, a male was observed to connect with a female while lying underneath her. The ultimate position, however, was normal.

The period of copulation is usually lengthy, lasting from one to two days. After having been connected to a female for a day or two a male will release himself only to renew the copulatory act half an hour or so later, and frequently with the same female. It is difficult to assign a reason for the apparent incomplete consummation of the act of copulation which seems to occur in such a case. When *in coitu* the female drags the male, apparently against his will, from place to place, or merely rests in one position and feeds. The male has not been observed to feed while copulating.

In the field, about the time for oviposition, females may be seen wandering about on bare ground or among the grass in search of a suitable spot for their ova. On 23rd January a mass of ova was found in the field deposited in a small cavity on the south-west side at the base of a *Hydnocarpus anthelmintica*. This was the only mass found. In less sheltered positions it is likely that the female covers her ova with soil. In the laboratory ova were occasionally placed in fissures in decaying *H. anthelmintica* fruits. The ova are deposited in loosely adhering masses containing from 110 to 180.

By 17th January *M. faber* had become less numerous. This was partly due to natural causes, but very largely to control measures, which consisted of spraying with kerosene emulsion and with a pyrethrum solution. In addition, large numbers were collected daily and destroyed by immersion in kerosene and water, a method of control which can be carried out without difficulty, since *M. faber* is more or less gregarious throughout its life-cycle.

Larvae in the second instar were observed in the field on 27th January and at that time appeared to be about two days old.

Occasionally this species will vary its diet by sucking its own ova, considerable numbers of which have been found in the breeding cages empty. It is probable that if the ova were fixed to the spot on which they were deposited and were thus in a stable position, far greater numbers would be destroyed. As it is, the ova being deposited in loose masses, the insects experience great difficulty in preventing an ovum, which it desires to suck, from sliding away from the tip of the rostrum, when pressure is applied.

In the field, on one occasion an adult female was found sucking a 4th instar larva of its own species.

Large numbers of *M. faber* of both sexes were placed under observation in the laboratory. The females oviposited freely, but out of several hundred ova only two larvae were obtained, and they died shortly after eclosion. The principal obstacle one encounters in attempts to rear this insect from the ovum is the regulation of the atmospheric conditions in the breeding cages. Most of the ova obtained in the laboratory were placed on damp filter paper in petri dishes. Only two larvae were obtained from them, and these, as previously stated, died. The greater number of the ova developed mould, and the remainder collapsed and shrivelled. Another batch of ova were placed in shallow depressions in damp soil and lightly covered with soil, but mould again made an appearance.

Mortality among ova and larvae in the field would appear to be high also, for from the ova which were presumably deposited by the several hundred adults remaining on or in the vicinity of the *Hydnocarpus* trees, very few larvae could have emerged successfully, judging by their scarcity about the middle of March. Larvae brought into the laboratory throve fairly well, but several failures to carry out ecdysis successfully were noted.

Shortly before eclosion, pale reddish-orange patches can be seen showing through the chorion, which is split irregularly by the emerging larva and afterwards shrivels.

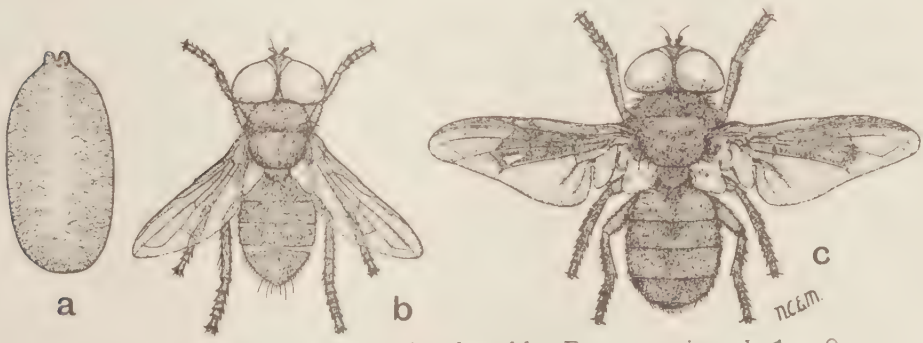


Fig. 1. Tachinid parasite of *Melamphaus faber*, F.: *a*, puparium; *b*, ♂; *c*, ♀.

There was considerable mortality in the laboratory among the adults brought in from the field, and dissections of some of the dead females were made. Judging by the great distension of the abdomen of most of these females, their demise was almost certainly due to congestion of the ovary. The crop and rectum were also strongly distended with a brownish creamy substance which, when beaten up in water, yielded a quantity of clear yellowish globules of oil. The ovary consists of fourteen ovarioles.

In the laboratory, oviposition usually took place in the evening, between five and six o'clock, the ova being deposited on the floor of the breeding cage, as a rule.

Very little is known at present regarding the natural enemies of *M. faber*, which, owing to its objectionable smell, presumably is rarely attacked by birds or mammals.

It is attacked, however, by an unidentified Tachinid fly (fig. 1). From about two hundred and fifty adult *M. faber* captured in the field, five puparia of this Tachinid were obtained. From these a male and a female emerged successfully, but the remaining three died. The larva of this fly leaves its host shortly before the formation of the puparium, which when fully formed weighs about a third of the weight of an adult female *M. faber*. The pupal period lasts for fourteen days.

It has not been possible to obtain definite details regarding the duration of each individual stage of the life-history of *M. faber*, but from observations made in the field, the life-cycle from the date of oviposition to the adult stage is from 60 to 70 days. The incubation period in the laboratory was 11 days.

A female *M. faber* has been captured at light in Kuala Lumpur, F.M.S., by Capt. H. M. Pendlebury, Systematic Entomologist, Federated Malay States Museums.

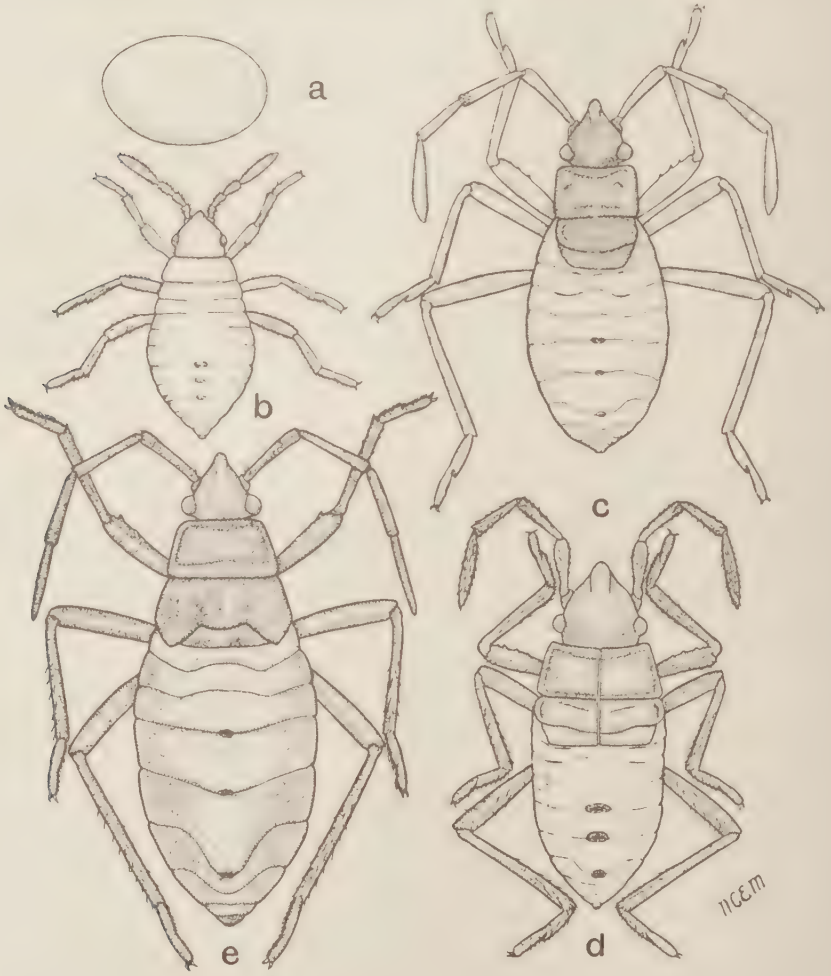


Fig. 2. *Melamphaus faber*, F.: *a*, ovum; *b*, 1st instar; *c*, 2nd instar; *d*, 3rd instar; *e*, 4th instar.

Developmental Stages of Melamphaus faber, F.

Ovum (fig. 2, *a*).

Opalescent, smooth, shining; regularly ovate and very feebly reticulate. Chorion moderately soft. 1·8 × 1 mm.

First Instar (fig. 2, *b*).

Whitish. Eyes red. Antennae feebly infumate basally, metanotum laterally, and abdomen suffused with pink ; area around dorsal plates whitish. Setae and legs brown.

Elongate ovate. Abdomen convex dorsally and dorso-ventrally compressed laterally. Dorsal plates on segments 3, 4 and 5. Legs with moderately stout setae. Length 2·5 mm.

Second Instar (fig. 2, *c*).

Antennae pale olivaceous ; basal two-thirds of segment 2, whitish. Head and nota piceous, with faint reddish tinge. Abdomen red ; dorsal plates blackish. Legs whitish, irregularly suffused with olivaceous ; setae on tibiae dark brown and fulvous. Abdomen globose, smooth and shiny, moderately covered with short fulvous setae. Lateral margins of metanotum irregular. Length 3·5 mm.

Third Instar (fig, 2, *d*).

Antennae blackish ; segment 2 white in basal half ; base of segments 3 and 4 with faint vinaceous suffusion ; segments 1 and 2 sparsely, segments 3 and 4 rather thickly setose ; setae on segments 1–3 blackish, on segment 4 fulvous. Eyes light red. Head and nota blackish. Legs infumate ; tibiae and tarsi paler then femora. Abdomen light red, except segment 9 which is black ; dorsal plates piceous ; segments 1 and 2 with a small elongate piceous spot laterally on posterior margin ; abdomen dorsally and ventrally sparsely covered with fine short fulvous setae. Sternites and rostrum infumate.

Elongate ovate, smooth and shiny. Posterior margin of anterior femora with some short stout spines. Rostrum reaching the posterior margin of 6th abdominal segment. Basal segment of antennae somewhat swollen apically and feebly curved. Integument very soft.

The resemblance between the larva of this instar and that of the 2nd instar is very close. The dorsal plates in this instar are broader and the abdomen is less globose and dorso-ventrally compressed laterally. Length 7 mm.

Fourth Instar (fig. 2, *e*).

Antennae piceous ; segment 2 with a white longitudinal stripe on upper surface of basal half ; segment 1 apically, segments 2–4 basally and apically with narrow vinaceous suffusion. Eyes dark red suffused with black. Upper surface of head piceous ; lower surface paler with a reddish tinge. Nota reddish piceous. Segments 1–3 of abdomen dorsally light red ; segment 1 almost entirely suffused with brown ; segment 2 with a brown suffusion laterally ; segment 3 similar to segment 2 but with a whitish transverse patch on posterior margin laterally ; remaining segments except 9 light red with a broad pruinose suffusion laterally and a whitish suffusion on posterior margin laterally ; external margin of connexivum of all segments except 9, pinkish ; area around dorsal plates black. Sternites light red. Legs and rostrum piceous. Abdomen ventrally light red, with a broad pruinose suffusion laterally on segments 3–6 ; posterior margins of segments 3–5 narrowly white ; segments 5–8 with a blackish spot mid-ventrally at anterior margin. Setae on legs and antennae black.

Rostrum reaching almost to posterior margin of segment 4 ; rudiments of hemielytra visible. Sensory hairs and pits are present on the ventral surface of the abdomen in the following positions : two subventrally near anterior margin and four subventrally but closer together near posterior margin on segment 2 ; six subventrally near anterior margin of segment 3 ; three laterally at anterior margin of segment 4 ; one laterally at anterior margin of segment 5 ; three laterally at anterior margin and three laterally at posterior margin of segment 6. Length 12 mm.

Fifth Instar (fig. 3, *a*).

Antennae and legs piceous. Eyes dark red with a blackish suffusion. Nota and rudimentary hemielytra reddish with black suffusion. Segment 1 of the abdomen dorsally red, with two quadrate black spots subdorsally; segment 2 red, with pruinose suffusion laterally; segment 3 red, with black suffusion laterally and narrowly along posterior margin, except laterally where whitish; segments 4 and 5 red, broadly black laterally and with a transverse whitish spot on posterior margin laterally; segment 6 reddish or purplish black; ventral surface of abdomen light red with transverse white suffusion on posterior margin of segments 3–5; segment 3 feebly, remaining segments strongly suffused with black laterally; trichobothria at anterior margin of segment 4 enclosed in brown suffusion; segments 5 6 with a dull blackish spot; segments 7 and 8 with a shining black spot mid-ventrally. Ventral surface of head and sternites light red. Setae on antennae and legs fulvous.

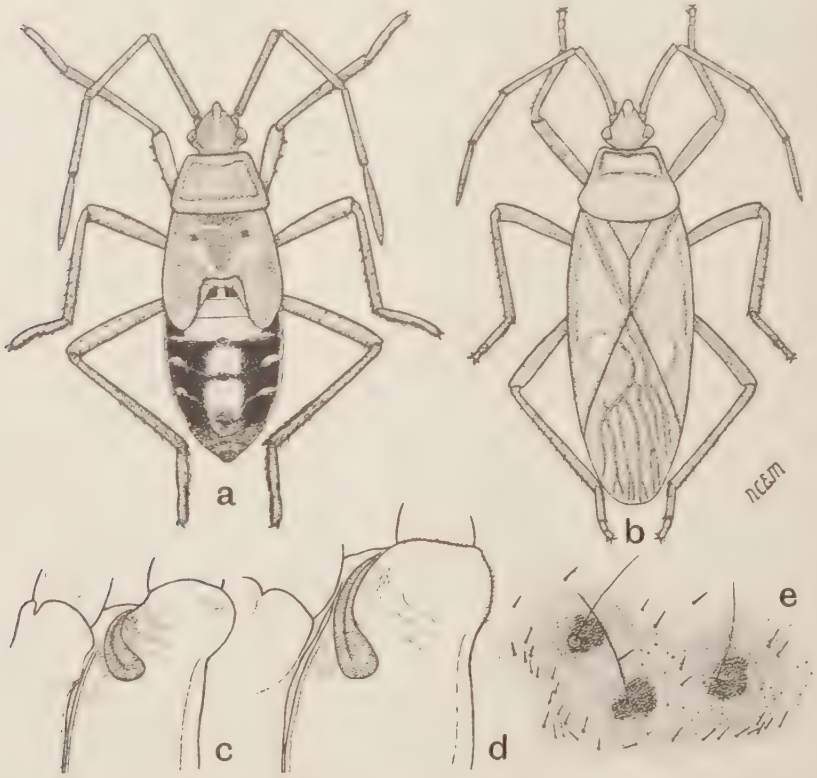


Fig. 3. *Melamphaus faber*, F.: *a*, 5th instar; *b*, adult; *c*, metasternal gland orifice ♂; *d*, metasternal gland orifice ♀; *e*, trichobothria on abdomen.

A variety has the abdomen entirely red and the head, nota and rudimentary hemielytra dark piceous. This variety gives rise to the adult having the head, anterior half of pronotum and whole ventral surface red.

Rostrum reaching almost to posterior margin of 4th abdominal segment. Rudimentary hemielytra reaching almost to posterior margin of segment 3 of abdomen. Head, nota and rudimentary hemielytra densely pilose. Length 16 mm.

Adult (fig. 3, *b*).

Segments 1–3 of antennae black; segment 4 greyish with a narrow transverse black band basally. Eyes brown. Head, pronotum and hemielytra black; sides of juga, tylus and antenniferous tubercles with a fine fulvous pubescence. Pleura blackish brown, with a fine fulvous pubescence. Abdomen dorsally light red; connexivum orange; abdomen ventrally red, with purplish black suffusion subventrally and with a black spot near anterior margin on each side of mid-venter, and two black spots subventrally but more widely separated than those near anterior margin, on segment 3; a black spot near anterior margin of segment 4; a black spot laterally on segments 5–6 near anterior margin and a black spot sublaterally near posterior margin on segments 6–7. These black spots surround trichobothria (fig. 3, *c*). Coxae light brown; legs black; rostrum shining black. Meso- and metathorax and base of corium, reddish orange. Wings pale brownish ochreous and faintly infumate. Corium black; membrane dark brownish ochreous.

Four colour varieties have been captured in the field. The outstanding differences from the typical *M. faber* may be summarised as follows:—

(1) Head, anterior half of pronotum, pleura red. Corium with an orange-red spot at middle of apical margin.

(2) Similar to (1) but with the spot on corium indistinct.

(3) Anterior and lateral margins of pronotum in anterior half, red.

(4) Ventral surface of abdomen with a transverse blackish suffusion on each segment.

Length, ♂, 21–22 mm.; ♀, 24·5–26·5 mm. Width between pronotal angles, ♂, 6–6·7 mm.; ♀, 7·5 mm.

NOTES ON THE NATURAL ENEMIES OF THE SUGAR-CANE FROGHOPPER (*TOMASPIS SACCHARINA*, DIST.) IN TRINIDAD, WITH DESCRIPTIONS OF NEW SPECIES.

By Alan Pickles, B.Sc., A.I.C.T.A., F.E.S.,

Entomologist, Trinidad Sugar-Cane Investigation Committee.

From the formation of the Froghopper Investigation Committee in 1925, the chemico-ecological relations of the froghopper have engrossed the greater part of the attentions of the scientific workers on this pest, and a considerable volume of precise knowledge on these lines has been accumulated by Hardy and his colleagues. From representations made by Dr. J. G. Myers, however, the necessity for more strictly entomological work was realised, work which should be "comparable in precision and in extent with that already amassed by the Committee."[4, 5] The present paper is an account of a part of the work undertaken with this somewhat ambitious end in view. The studies of which an account is given here were commenced in September 1929, but owing to absence on duty abroad, the real beginning of the work did not occur until March 1930.

An attempt was made, not only to determine what parasites and predators of *Tomaspis* occurred in Trinidad, but also to obtain numerical data illustrating their seasonal and geographical distribution and their relative abundance and efficiency.

Methods adopted.

As the investigations in Trinidad had to be commenced during the dry season, a time when nymphs and adults of *Tomaspis saccharina* are exceedingly scarce, attention was first paid to a survey of egg parasites. It was already known[10] that the eggs of this froghopper are laid in the adhering trash of canes and also in the surrounding soil. Later it was shown that eggs were relatively scarce in the trash but were abundant in the soil of affected fields, and a technique was devised to isolate them.[7] Eggs so obtained were counted and set to hatch on damp blotting paper enclosed in small glass culture-dishes. The cultures were examined daily for signs of parasitism and were re-moistened from time to time as required. Soil samples were collected for this examination from as many localities as possible in each month of the year. So far as possible, the same fields were selected for study on each visit, but this plan had to be modified occasionally in consequence of agricultural operations. The chief impediment to accuracy of the resulting figures for the percentage parasitism is the utter impossibility of obtaining the same number of eggs in every sample. Until the sample has been prepared and examined in the laboratory, it is quite impossible for the observer to know how many eggs have been obtained, and the number collected may vary from few or none to over a hundred per sample. As experience was gained, however, this difficulty diminished in importance.

From the earlier published work,[3] it was seen that the most important enemy of the post-embryonic stages is the predacious larva of a Syrphid fly, *Salpingogaster nigra*, Schiner. In order to evaluate the relative abundance of this predator, large quantities of froghopper nymphs with their entire spittle-masses were collected, and the number of both nymphs and Syrphids was obtained. The nymphs were collected without examination into cigarette tins, fifty in each, and the counts were made in the laboratory. So far as possible, four fields from each estate were visited, taking a minimum of one hundred nymphs from each field. In uncultivated localities, a minimum of two hundred nymphs was examined. During interbrood periods, these

conditions could not always be satisfied. Later, when the aid of competent assistants was available, some of the counts were made directly in the field. In this way, the abundance of Syrphids relative to froghoppers was found and an idea was obtained of the regularity of the Syrphid distribution in the area.

Descriptions of new Egg Parasites.

Anagrus urichi, sp. n. (MYMARIDAE).

♀ (fig. 1, *a*).—Head, thorax, legs, and scape and pedicel of antennae, golden yellow; abdomen and funicle of antennae fuscous; eyes and ocelli red.

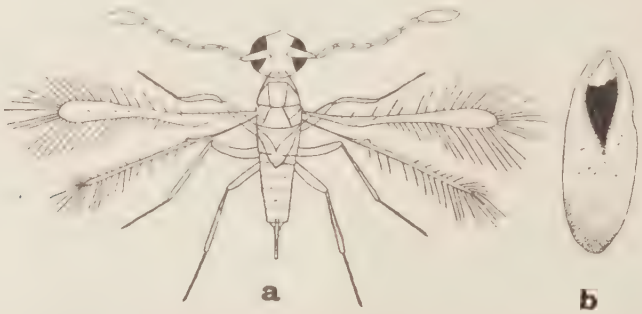


Fig. 1. (*a*) *Anagrus urichi*, sp. n. adult female; (b) *Tomaspis saccharina*, Dist., eggshell after emergence of *Anagrus urichi*.

Antennae with the bases widely separated, close to the eyes. Frons with eight setae, *viz.*, three anterior on each side and a pair between the antennae; vertex bearing the ocelli in its posterior angle, remote from the eyes; ocellar triangle very compact and bearing four setae; four stout setae on each ocular sclerite. Antennae (fig. 2, *a*) but little shorter than the body (8 : 9), terminal segment enlarged; scape with two or three short hairs, pedicel devoid of hairs, funicle with a sparse covering of short hairs; scape rather long, about 2·25 times the length of the pedicel; pedicel twice as long as the first funicular segment, which is short and has a narrow base and broad apex; second segment of funicle more than twice as long as the first; second to sixth segments progessively increasing slightly in length and breadth, relatively stout, the length of any segment never exceeding three times the greatest breadth; terminal segment twice as long as sub-terminal. Mandibles (fig. 2, *c*) with two teeth, the ventral tooth bicuspid; outer margin bearing a few small hairs.

Thorax with a light sculpturing on the scutum and parapsides—that on the parapsides forming more or less equal-sided cells, that on the scutum enclosing longitudinally elongated areas; pronotum with a single seta in each posterior arm; two anterior and two posterior bristles on the scutum, their bases forming a square; a bristle in the external angle of each parapsis and one on each axilla; axillae not acutely produced forward into the parapsides.

Forewing (fig. 2, *d*) with the anterior margin concave, expanded near the apex, and the posterior margin expanded slightly beneath the marginal vein; marginal fringe long, the longest seta (sub-apical in position) nearly one-third the total length of the wing; three series of short setae on the disk, two near the apical margin, continuing around the apex, and a median series of five or six setae not extending to the apex or to the level of the marginal vein; apical margin of wing slightly infuscated; length 0·46 mm., greatest breadth 0·05 mm. Hind wing (fig. 2, *e*) linear, petiolate at the base; marginal fringe much longer behind than in front (3 : 1), an abrupt change in the length of the setae occurring at the apex; a few short discal

bristles near the margins, about the middle of the length of the wing ; a median row of discal bristles running from the level of the marginal vein to within a short distance of the apex ; anterior margin elevated at the tip of the marginal vein and bearing three short setae at this point ; length 0·41 mm., greatest breadth 0·017 mm.



Fig. 2. *Anagrus urichi*, sp. n.: (*a*) antenna of ♀; (*b*) antenna of ♂; (*c*) mandible of ♀; (*d*) left forewing of ♀; (*e*) left hindwing of ♀; (*f*) right anterior leg of ♀.

Anterior tibiae (fig 2, *f*) with a large, plumose apical spur, and first tarsal joint of these legs with about 12 rather stiff, short bristles opposing it ; remaining tibiae with a rather prominent, simple apical spur, not opposed by tarsal bristles ; coxae broad and mobile, not contiguous on either side ; trochanters 2-jointed ; tarsi 4-jointed.

Abdomen broadly sessile, the ovipositor issuing near its base.

Length 0·51 mm., expanse 1·05 mm.

♂.—Yellowish brown, abdomen somewhat darker ; eyes and ocelli red. Antennae (fig. 2, *b*) not sensibly shorter than the body, composed of thirteen segments ; bases widely separated ; scape 1·5 times as long as pedicel and the latter twice as long as the first funicular segment ; first five segments of funicle progressively increasing slightly in length, the sixth rather shorter than the fifth and equal to the fourth ; sixth to eleventh segments again increasing progressively, the terminal one twice as long as the first ; length of funicular segments not more than three times the greatest breadth ; total length 0·41 mm. Similar to the female in other respects, except for the relations of the genitalia.

Length 0·41 mm., expanse 0·91 mm.

I have pleasure in naming this species after my friend and former tutor, Mr. F. W. Urich, who was the pioneer of froghopper research in Trinidad.

Dr. Ferrière states that this species is very closely allied to *A. flaveolus*, Waterh. (from eggs of *Peregrinus maidis* in Trinidad) and *A. armatus*, Ashm., but differs from them both in the very sparse discal ciliation of the wings.

Abbella tomaspidis, sp. n. (TRICHOGRAMMATIDAE).

♀. -Brown to golden brown, the abdomen and funicle of the antennae darker, legs paler, eyes reddish black, ocelli red.

Orbits slightly divergent before and behind their equators ; ocellar triangle short, the pair about two diameters from the orbits and from each other. Clypeus produced acutely between the antennae. Chaetotaxy of head : two bristles behind the median ocellus, three between each of the pair and the orbits, one on the posterior part of the vertex on each side near the orbits, four on the disk of the clypeus and two in its prolongation between the antennae, seven on each gena, two on the labrum, in its posterior angles. Antennae with eight segments, length 0·29 mm., scape about twice the pedicel, ring-joints minute, the two proximal joints of the club short and broad, about one-fourth the pedicel, the distal one slightly the longer, third club joint much longer (about 6 : 1), truncated conical, terminal joint one-sixth longer again, conical, acute. The funicle segments bear large sensoria, small sutural sensoria, and long, rather stout bristles (fig. 3, *a*). Mandibles tri-dentate, the teeth short (fig. 3, *b*).

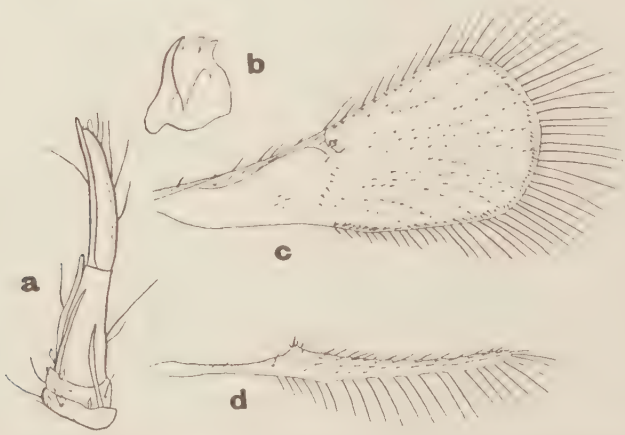


Fig. 3. *Abbella tomaspidis*, sp. n. : (*a*) funicle of antenna ; (*b*) mandible ; (*c*) right forewing ; (*d*) right hindwing.

Thorax with the protergites triangular, bearing each two anterior bristles, and with a reticulate pattern, the cells but little longer than broad. Mesonotum with a reticulate sculptured pattern, the cells elongate hexagonal, pattern extending on to the propodeon. Four bristles on the mesonotum, two on each parapsis, four on the scutellum and three on the propodeon (one before the spiracle and two behind).

Length of forewing more than twice the greatest breadth (5 : 2), length 0·50 mm., longest cilia of fringe one-half the greatest width of the wing (fig. 3, *c*). Hindwings (fig. 3, *d*) 10–11 times the greatest width, length 0·44 mm., three rows of discal cilia, the posterior row not continued to the wing apex.

Fore legs 0·42 mm. long ; coxa two-thirds of the femur and three-fourths of the tibia. Middle legs 0·49 mm., femur twice the length of the coxa, tibiae very long and slender, about one and two-thirds the length of the femur and nearly one-third the

total length of the leg. Hind legs 0·54 mm. long, femur slightly shorter than the coxa, tibia and tarsus more or less equal, forming together more than half the total length of the leg.

Length of abdomen 0·32 mm., segments sub-equal, sparsely hairy.

Total length 0·64 mm., expanse 1·33 mm.

Described from two female specimens, one reared from the egg of *Tomaspis saccharina*, Dist., one bred from grass infested by this froghopper in an abandoned cane-field.

The generic position of this species has been kindly determined by Dr. Ferrière, Imperial Institute of Entomology.

Observations on Egg Parasites.

The occurrence of *Abbella tomaspidis* may be dismissed briefly, as it was only encountered on three occasions. The first specimen was reared from an egg of *Tomaspis saccharina* collected from farmer's canes at Caroni Savannah, in March 1930, being indeed the first egg parasite encountered in the present survey. A second specimen was bred from grass roots taken from an abandoned field at Woodford Lodge Estate. The third (mutilated) specimen was found in an egg from Usine Ste. Madeleine, from which it had failed to emerge.

Anagrus urichi, on the contrary, was frequently observed. Table I summarises the observations on this species to date. From this it is evident that the occurrence of the parasite is extremely irregular, and no conclusions as to the factors governing its distribution can be deduced from the figures.

TABLE I.

Showing the Occurrence of Anagrus urichi *on Cane Estates, March 1930-March 1931.*

	1930										1931		
Estate.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov	Dec.	Jan.	Feb.	Mar.
Orange Grove	0	0	0	0	0	0	0	2·9	0	0	0	0	0
Caroni ...	0	2·5	0	0	0	0	0	5	0·6	1·8	0·4	3·8	0
Woodford Lodge	0	0	0	33	0	11	0	0	1·4	0	0	0	0
Felicite ...	0	0	0	0	0	3·4	0	0	0	0	4·5	0	0
Waterloo ...	—	—	—	—	—	—	—	—	—	—	1·0	0	0
Brechin Castle	0	0	0	0	0	1·2	0	0	0	0	0	0	0
Esperanza ...	—	—	—	—	0	0	1	0	5	0	0	0	0
Forres Park ...	—	—	—	—	—	—	—	—	—	—	0	0	0
Ste. Madeleine	0	0·7	0	0	0	0	0	4/14	0	0	0	0	0

The incidence of 33 per cent. recorded from Woodford Lodge in June 1930 requires some explanation. There is reason to believe that the development period of the parasite is considerably longer than the incubation period of the average froghopper egg. The eggs laid by the first brood, which are involved here, nearly all hatch after 14–20 days incubation.[13] Towards the end of the second brood, therefore, the only eggs remaining in the soil will be the small proportion of so-called " long-period eggs " and eggs which are parasitised. It thus follows that figures for parasite incidence taken at such a time will give a false impression of the activity of the parasite. Similar considerations doubtless apply to the later broods, but as the proportion of long-period eggs increases later in the year, the error will not be so marked. The table shows that at no time is the parasite generally abundant, and its incidence is never great enough to exert an appreciable check on the froghopper's increase.

Similar observations have been made in areas other than sugar estates, in the course of which some 1,500 eggs have been examined. None of these up to the present has yielded parasites, with the exception of a forest area between Moruga and Guayaguayare, where 10 per cent. of the eggs were attacked. The parasite concerned in this case, however, seems to differ in some respects from *Anagrus urichi* and is possibly a distinct species.[6]

Three individuals of *Anagrus urichi* usually develop within one egg. In approximately half the eggs, one of these is a male, so that the ratio of females to males would appear to be about five to one. Emergence takes place through the hatching lid of the egg (fig. 1, *b*), through which a small irregular hole is bitten. Since the hatching lid easily becomes detached from an empty egg envelope, it is not possible to learn much of the parasite incidence from an examination of hatched eggs.

Oligosita giraulti, Crawford, the so-called "Vermilion Parasite," was discovered by Guppy and has received a good deal of study from Urich[9, 11] and from Williams.[14, 15] Unfortunately, most of the records of this insect refer to parasitism in captivity only, the usual procedure being to breed miscellaneous parasitic Hymenoptera from grass, any likely insects emerging being then caged with froghopper eggs.[15] In captivity, about 20 per cent. of the eggs are attacked. Kershaw, however, by searching for froghopper eggs in grass found 5–10 per cent. to be the maximum parasitism, with the average probably below 5 per cent. He concludes: "I consider it probable that this parasite is really on some other host, and only occasionally attacks the froghopper."[3]

In the course of the present survey, many attempts were made to discover localities for this parasite without success. Urich discovered one specimen at Caura in November 1929, but repeated search in this locality failed to bring further specimens to light. About 400 froghopper eggs from stations in the Northern Range hills have been examined to date, but none of these has shown any indication of parasitism by *Oligosita*. *Oligosita* was also recorded from cane estates by previous workers, but in the present survey, none of the 10,000 eggs examined from cane estates was parasitised by this species.

Observations on Predators.

As stated above, the chief predacious enemy of *Tomaspis saccharina* is the larva of *Salpingogaster nigra*, Schiner. The life-history of this species has been worked out by Guppy,[1, 2] who also attempted, without success, to rear the insect in captivity in quantities sufficient for liberation in the cane fields early in the season.

Kershaw[3] points out that *Salpingogaster* only appears in numbers on the later broods of froghoppers, chiefly the third, by which time a considerable amount of froghopper damage has already occurred.

Table II shows the Syrphid incidence as observed at various stations in the course of the present survey. The incidence is expressed as the number of Syrphid larvae per hundred froghopper nymphs. These figures show a greater degree of regularity than is indicated by the figures for the parasitism of eggs, and it is probable that the regularity may be greater still in a year in which the fluctuations of rainfall are less erratic than in 1930.

From the figures it is seen that Syrphid incidence was appreciable only on two estates in July, and did not become general until August and September. In October, a rapid falling off in the Syrphid population occurred, and Syrphids were seen only on one estate after this month. The Syrphid population was thus only significant during the third brood in most localities.

At Woodford Lodge Estate, however, the greatest Syrphid population occurred before the end of the second brood. In one field at this time, the incidence amounted to 12 per cent., and this field was kept under special bi-weekly observation in order to

ascertain if such a density of predators could exterminate the froghopper nymphs present. Guppy[4] states that one Syrphid larva in the course of its life destroys 30–40 froghopper nymphs. A Syrphid incidence of at most 5 per cent. should, therefore, be able to destroy the froghopper population in one locality, and one of 12 per cent. might therefore be expected to be thoroughly efficient in this respect. Unfortunately, however, an unexpected period of severe drought occurred soon after this was noted, and both nymphs and Syrphids quickly disappeared, though not until a very large froghopper population had reached the imaginal condition. At present, therefore, it is impossible to say whether or no Syrphid larvae under the most favourable field conditions could bring about economic control of the froghopper.

TABLE II.

Showing the Occurrence of Salpingogaster *Larvae on Estates, March 1930-March 1931.*

	1930										1931		
Estate.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.
Orange Grove	0	0	0	0	0	0·4	0	5·0	0	0	0	0	0
Caroni ...	0	0	0	0	0	3·0	1·0	1·0	0	0	0	0	0
Woodford Lodge	0	0	0	0·8	9·0	3·4	3·0	1·0	0	0	0	0	0
Felicite ...	0	0	0	0	0	2·3	1·3	1·0	4·8	1·0	0	0	0
Waterloo ...	—	—	—	—	—	—	—	—	—	—	0	0	0
Brechin Castle	0	0	0	0	1·0	2·0	2·5	0	0	0	0	0	0
Esperanza ...	0	0	0	0	0	0	0	0	0	0	0	0	0
Forres Park ...	—	—	—	—	—	—	—	—	—	—	0	0	0
Ste. Madeleine	0	0	0	0	0	1·6	slight	slight	0	0	0	0	0

Casual observation suggests that the *proportion* of Syrphids present increases with the froghopper population; that is, a badly attacked field will not only contain a greater number of Syrphids than one lightly infested, but also more *pro rata*. This point, however, requires further study.

Syrphid incidence at Esperanza Estate and at the estates of the Ste. Madeleine Sugar Company seems to be very low. No Syrphids were encountered in the former locality, though it must be admitted that no special endeavour, beyond the routine investigation, was made to find them on this estate. At Ste. Madeleine, however, an additional method of study suggested itself. Light trapping of froghoppers is practised on this estate, and examination of a small portion of the captures showed that Syrphid adults also were included in the traps. The entire catches on three nights were therefore examined, comprising about 34,000 froghoppers in all. The proportions of adult Syrphids were successively 0·025 per cent., 0·010 per cent., and 0·009 per cent., indicating that the Syrphid incidence is probably very low on this estate. No opportunity has occurred of comparing these results with those from other localities. These figures are quoted merely as a slight confirmation of the larval counts. In the absence of critical studies on the phototropic behaviour of *S. nigra*, little significance can be attributed to light trap examinations alone.

On uncultivated land, Syrphid incidence of much the same order of magnitude occurs. The possibility of *Tomaspis saccharina* being originally a forest insect has been discussed elsewhere,[6, 14] and in moist, shaded situations where *Tomaspis* occurs throughout the year, its Syrphid predator occurs in small numbers even in the driest months. It is unfortunate that owing to the difficulty and expense of making regular visits to suitable natural localities, the records for Syrphid incidence are by no means so complete for such places as they are for the cane estates.

In Trinidad, *Salpingogaster nigra* seems to be an almost specific predator of *Tomaspis saccharina*. In the course of the present investigations, *Salpingogaster* has

been found on two occasions in spittle-masses of *Tomaspis pubescens*, Fabr., *i.e.*, two Syrphids out of the 1,500 spittle-masses of this species examined. Guppy[2] mentions that it is not possible to utilise *T. pubescens* for rearing the Syrphid in captivity, partly because it does not thrive on this host. The third common species of *Tomaspis* in Trinidad, *T. rubra*, Linn., has its own Syrphid predator, *Salpingogaster ? pygophora*, Schiner, discovered by Urich,[12] and *S. nigra* is not known to attack it.

No systematic study of "Jumping Spiders" (Attidae) was made. One undetermined species, however, occurred at Woodford Lodge Estate in some numbers, and was to be seen fairly frequently carrying off adult froghoppers. A specimen of the same species was also seen in roadside grass near Guayaguayare, in the act of bearing away an adult of *T. pubescens*.

An extensive list of the minor parasites and predators of *Tomaspis saccharina* is given by Williams.[14] No additional information can be given with reference to these. Scorpions were reported to be attacking adult froghoppers at Woodford Lodge Estate in August 1930.[8]

The author desires to express his gratitude to Dr. J. G. Myers, on whose suggestion the work was inaugurated, for his unfailing advice, assistance and criticism. Thanks are due also to Mr. F. W. Urich, whose lengthy experience of entomology and of agriculture in Trinidad has been of great assistance.

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SUPERPARASITISM BY *COLLYRIA CALCITRATOR*, GRAV.

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(With an Appendix by R. H. Stoy, B.A., Caius College, Cambridge.)

The term "superparasitism" was originally introduced by Fiske (1910, p. 89) to denote the condition that results "when any individual host is attacked by two or more species of primary parasites, or by one species more than once." It was later restricted by Smith (1916, p. 486) to "that form of symbiosis occurring when there is a superabundance of parasites *of a single species* attacking an individual host insect."

Fiske recognized (p. 91) that "the prevalence of superparasitism depends entirely upon whether or not the female parasite is gifted with a prescience which will enable her to select healthy hosts for her offspring." He observed faint indications of such a faculty in a very few species, but on the basis of his work at the Gipsy Moth Parasite Laboratory came to the conclusion that it was generally wanting. Fiske pointed out that the total absence of such an instinct would make the prevalence of superparasitism wholly dependent upon the law of chance. Developing this idea, he gave a brief mathematical treatment of the problem and a graph showing the parasitism to be expected when a number of parasite eggs are distributed at random, by chance, among a number of hosts.

Thompson (1924) elaborated Fiske's mathematics and, treating the distribution of the parasite eggs as a matter of chance, produced the solution :—

$$y = N(1 - e^{-\frac{x}{N}})$$

where N represents the number of hosts, x the number of parasite eggs distributed, y the number of hosts parasitized, and e the Napierian logarithmic base.

The present position, then, is that superparasitism has been observed and defined and, on the assumption that the parasite progeny are distributed at random, treated mathematically. Theory, it will be noticed, has far outstripped experiment; the assumption that parasitism is entirely governed by chance has not been experimentally examined and the end result, the superparasitism occurring in nature, has been merely observed, not measured. I hope to publish in the near future an experimental study of the problem. The purpose of the present paper is to record some quantitative data on natural superparasitism by the Ichneumonid parasite, *Collyria calcitrator*.

Collyria calcitrator, Gravenhorst, lays its eggs, in England, in the eggs of the wheat-stem sawfly, *Cephus pygmaeus*, Linnaeus. The sawfly hatches, completes its larval development, constructs its hibernaculum, and passes the winter with the parasite inside its body-cavity. The first and second larval stages of the parasite, found in the host larva during the late summer and early autumn, have dark sclerotic head-capsules provided with comparatively large mandibles. The third and fourth larval stages, found in the hibernating sawfly larva during the winter, are extremely flaccid forms without any conspicuously sclerotized or darkened parts. These larval stages have been described in detail elsewhere (Salt, 1931), here it is necessary only to call attention to the hard head-capsules of the first and second stages and to the fact that they do not immediately disintegrate when they are cast off by the developing larva but may be found, along with the third- or fourth-stage larva that developed from them, in the body-cavity of the host.

It often happens that more than one egg of the parasite is laid in a single *Cephus*, and in this case, since only one *Collyria* can develop in each host, all but one must die. Only once in over five thousand dissections have I found two living third-stage larvae together in one host. The elimination of the others usually takes place in the second larval stage, while the larvae are furnished with their powerful mandibles. Fortunately for our present purpose, when one second-stage *Collyria* larva falls victim to another, its head-capsule is not destroyed by the victor and, resisting disintegration, may be found along with the surviving parasite in the body-cavity of the host.

Elimination of rivals also takes place to a slight extent in the first larval stage. When this has occurred it is still possible to ascertain the fact by counting the first-stage head-capsules, but less accurately because, being smaller, they disintegrate more readily and also are harder to find. Fortunately, a reduction in numbers in the first stage is not common. In many cases I have carefully counted the first- and second-stage remains present in a single host, but only rarely have I found more first-stage head-capsules than second-stage, and from several observations I am convinced that by far the greater part of the fighting occurs in the second stage.

For several reasons then, *Collyria calcitrator* is a good subject for a study of natural superparasitism :—(1) Only one parasite can develop in each host ; (2) elimination of the excess parasites is confined to the first and second larval stages and takes place very largely in the second stage ; (3) the remains of the destroyed first- and second-stage larvae persist, so that it is possible to determine exactly the number of second-stage larvae originally present and, with a slight error, the number of first-stage larvae ; (4) owing to the long persistence of the first- and second-stage remains, determination of the number of parasite larvae originally present can be made over a long period and after there is no possibility of further attack.

To determine the frequence of superparasitism by *Collyria calcitrator*, 3,761 larvae of *Cephus pygmaeus* were dissected. Of these, 2,712, or 72·11 per cent. were parasitized by *Collyria*. Of the 2,712 parasitized *Cephus* larvae, 2,195 were infested with one, 332 with two, 98 with three, 49 with four, 18 with five, 7 with six, 4 with seven, 5 with eight, 2 with nine, 1 with eleven, and 1 with sixteen parasites. There were, then, 3,594 individuals of *Collyria calcitrator* distributed among the 3,761 hosts.

If the ovipositing parasite females were perfectly able to select unparasitized hosts for each of their offspring, no *Cephus* would contain more than one parasite, and the 3,594 individuals of *Collyria* distributed among 3,761 hosts would give a parasitism of 95·56 per cent. This is very far from the observed parasitism of 72·11 per cent. In any case, it is immediately apparent from the dissections that more than one egg is laid in many hosts.

On the other hand, if the 3,594 parasites were distributed one at a time purely by chance among the 3,761 hosts, there should result, according to Thompson's formula, a parasitism of 61·54 per cent., and only 2,315 hosts should be parasitized. With these values again, the observed parasitism of 72·11 per cent. and 2,712 individuals does not agree.

It appears from this superficial consideration, then, that neither random nor discriminate distribution completely explains the observed parasitism—the eggs do not seem to be distributed either perfectly wisely or entirely by chance. It is necessary, therefore, to consider the problem more closely to see whether either hypothesis can be modified so as satisfactorily to fit the observed parasitism.

Examining the problem from the mathematical side, it is desirable, of course, to be able to contrast *each* set of observed figures, the number of hosts containing 0, 1, 2, 3, and so on, parasites, with the corresponding number to be expected from the play of chance. Unfortunately, Thompson's formula allows a comparison of only the total number of hosts parasitized. At this point, therefore, I enlisted the aid of a

competent mathematician, Mr. R. H. Stoy, of Caius College, Cambridge, who kindly produced the solution explained in his appended note. His calculated values are contrasted with my observed figures in Table I.

The third column of Table I shows the number of hosts that may be expected to contain 0, 1, 2, and so on, parasites, when 3,594 parasites are distributed purely at random, one at a time, among 3,761 hosts. Comparing the observed figures with these values, we find the number of unparasitized hosts much too low and the number of hosts with only one parasite much too high. Indeed, these two numbers alone are sufficient to invalidate the hypothesis of purely random distribution. The numbers of hosts with two and three parasites are only about half the expected value and also

No. of parasites in a host	Observed number of hosts	Calculated number of hosts
0	1,049	1,446
1	2,195	1,382
2	332	660
3	98	210
4	49	50
5	18	10
6	7	2
7	4	0
8	5	0
9	2	0
10	0	0
11	1	0
12	0	0
13	0	0
14	0	0
15	0	0
16	1	0

TABLE I.—To compare the observed number of hosts containing 0, 1, 2, 3, and so on, parasites with the number to be expected when 3,594 parasites are distributed at random, one at a time, among 3,761 hosts.

argue against distribution by chance in favour of a certain amount of discrimination but, of course, flatly contradict the perfect selection of healthy hosts by the parasites. The number of hosts with four parasites agrees with the calculated value. All the more heavily parasitized hosts, those containing five or more parasites, are far too numerous for either hypothesis and count equally against both.

The mathematical analysis, then, shows clearly that random distribution of the eggs, one at a time, will not explain the observed parasitism. Further, in so far as the hosts containing 0, 1, 2, and 3 parasites are concerned, it suggests very emphatically that the ovipositing females are able, *at least to a certain extent*, to detect parasitized hosts and to avoid laying in them.

Turning now to criticize the observed data and to consider the problem from the entomological side, the following five points have to be taken into account.

First, the observational error is consistently negative. The first- and second-stage head-capsules are distinctive objects and nothing else in the body of the host could be taken for them and counted in their stead. On the other hand, they are comparatively small and are apt to be overlooked. A correction for this point, by decreasing the number of unparasitized hosts and increasing the number of hosts with one or more parasites would operate in favour of the hypothesis of random distribution in the hosts containing 2, 3, and 4 parasites, but against it in all the others ; and very

strongly against it in decreasing the number of unparasitized hosts, already far too small.

Secondly, it is likely that the parasite egg sometimes fails to hatch. A correction here would operate exactly as the one above but, since the chance of an egg failing to hatch in any particular host is obviously directly proportional to the number of eggs present, it would act more strongly in cases of heavy parasitism where already the observed numbers are too large.

Thirdly, the elimination of parasites in the first larval stage introduces an error which is actually a particular kind of observational error. Fortunately, as I have pointed out above, it is very slight. A correction for this point would increase the number of hosts containing two or more parasites and would therefore favour random distribution where there are 2, 3 or 4 parasites present, but oppose it where there are 5 or more.

Fourthly, the time occupied by the act of oviposition interferes with the strict application of the law of chance and requires a correction, if only a very slight one, in the calculated value. The duration of the egg-stage of *Cephus* is about eight days but, even if the eggs are suitable for parasitization throughout this period, which is unknown, their exposure to oviposition is much less, because *Collyria* females oviposit only three or four hours a day, while it is warm and bright. If there are dull or rainy days during the period, the exposure of the host is further reduced. Two females of *Collyria* scarcely could, even if they would, oviposit in the same *Cephus* egg at the same time. The adult parasites, indeed, take alarm at the approach of other individuals, and I think I am justified in assuming that in the great majority of cases the presence of one ovipositing female on the stem in the neighbourhood of a host egg precludes the presence of a second. Now the examination of the wheat stem ; the discovery of the host egg ; the assumption of the suitable attitude for oviposition including, as it very often does, a good deal of " fidgeting," cleaning of antennae and legs, and trial of several positions ; the perforation of the wheat stem ; the laying of the egg ; and often a delay in departure from the spot ; all of these actions take up an appreciable length of time. During this time other *Collyria* females are automatically excluded. This complete occupation of the host by the parasite temporarily removes the host from the free play of chance and consequently to some extent reduces the actual amount of superparasitism. A correction for it, therefore, would favour the hypothesis of random selection in hosts containing 2, 3, and 4 parasites, but oppose it in those containing 5 or more.

Fifthly, excessively superparasitized hosts may sometimes succumb to their condition. In the course of my dissections I have noted that full-grown *Cephus* larvae containing the remains of seven or eight parasites are sometimes quite apparently sickly. It is very likely that younger sawfly larvae containing several parasites may die, and even more likely that *Cephus* eggs containing too many *Collyria* eggs may be unable to develop. It is possible, too, that host eggs occasionally succumb simply to the too numerous perforations by the ovipositors of the parasites. This factor also operates to reduce the number of heavily parasitized hosts, and a correction for it would operate directly against the hypothesis of random distribution.

These five points act partly in favour of random and partly in favour of discriminating distribution. It is impossible at present to measure their several effects and the weight to be placed upon them is a matter of opinion. In any case, however, it is certain that none of these points will correct the observed data so much as to make them coincide with the calculated values, indeed, the only one of any considerable importance, the observational error, is opposed to the hypothesis of random distribution.

Neither mathematical nor entomological considerations, then, serve to bring the observed and calculated values into agreement. The hypothesis that the

eggs of *Collyria* are distributed one at a time purely by chance, therefore, is untenable.

On the other hand, it appears from the mathematical analysis, especially from a consideration of the numbers of unparasitized hosts and those containing only one parasite, that the ovipositing females are able, at least to a certain extent, to select unparasitized hosts for their offspring. Their ability, however, is obviously imperfect.

It should be noted that although this question of the ability or inability of the female parasites to select healthy hosts for their offspring is of considerable interest to the biologist, it is of little importance to the economic entomologist for, as Thompson (1924) has pointed out, the time required for control in the two cases is not greatly different.

Summary.

(1) It has been assumed that parasites oviposit in their hosts purely at random, not discriminating between healthy hosts and those already parasitized.

(2) Only one *Collyria calcitrator* can develop in each *Cephus pygmaeus* so that parasites of this species ovipositing in hosts already parasitized endanger or doom their progeny.

(3) 3,761 larvae of *Cephus pygmaeus* were dissected; 1,049 were unparasitized and 2,712 were parasitized by *Collyria calcitrator*; 2,195 contained one, 332 two, 98 three, 49 four, 18 five, 7 six, 4 seven, 5 eight, 2 nine, 1 eleven, and 1 sixteen parasites.

(4) These observed data do not agree, even when corrected for several factors, with the values to be expected from random distribution of the eggs one at a time.

(5) The observed data indicate a degree of discrimination on the part of the ovipositing females.

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APPENDIX.

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Deduction of the Mathematical Formula.

If the eggs are assumed to be distributed at random, one at a time, among the hosts, it is possible to calculate their most probable distribution mathematically.

Suppose there are x eggs distributed among N hosts. It is required to find the probable number of hosts that will receive p eggs.

The probability that any particular host receives any particular egg is $\frac{1}{N}$, and the probability that it does not receive this egg is $\frac{N-1}{N}$. To get the probability that any particular host receives a particular set of p eggs, we multiply the probabilities that it receives these eggs and the probabilities that it does not receive the other $(x-p)$ eggs together, as all these probabilities are supposed to be independent. Hence this probability is

$$\left(\frac{1}{N}\right)^p \left(\frac{N-1}{N}\right)^{x-p}$$

But it is possible to choose a set of p eggs out of a set of x eggs in ${}^{x}C_{p}$ ways,* so that the probability that any host receives p eggs is

$${}^{x}C_{p}\left(\frac{1}{N}\right)^p \left(\frac{N-1}{N}\right)^{x-p}$$

But there are N hosts in all, so the probable number of these N hosts to receive p eggs, when x eggs are distributed among them at random, one at a time, is

$$N\,{}^{x}C_{p}\left(\frac{1}{N}\right)^p \left(1-\frac{1}{N}\right)^{x-p}$$

* $${}^{x}C_{p} = \frac{x(x-1)(x-2)\ldots(x-p+1)}{p(p-1)(p-2)\ldots 1}$$

In particular, the number of hosts which remain unparasitized is given by putting $p=0$, *i.e.*, this number is

$$N\left(1-\frac{1}{N}\right)^x \text{ or } N\left[\left(1-\frac{1}{N}\right)^N\right]^{\frac{x}{N}}. \quad \text{Now } \operatorname*{Lt}_{N\to\infty}\left(1-\frac{1}{N}\right)^N = e^{-1}$$

where e is the Napierian logarithmic base, so that if N is large, the number of unparasitized hosts is very nearly $N\,e^{-\frac{x}{N}}$, and the number of parasitized hosts is therefore very nearly $N(1-e^{-\frac{x}{N}})$, which is Thompson's formula.

This approximate formula is accurate enough for all practical purposes. For example, in the case of Dr. Salt's data, the number of unparasitized hosts calculated by the exact formula $N\left(1-\frac{1}{N}\right)^x$ is $3761\left(1-\frac{1}{3761}\right)^{3594} = 1446{\cdot}1$, while using the approximate form $N\,e^{-\frac{x}{N}}$ it is $3761\,(e^{-\frac{3594}{3761}}) = 1446{\cdot}5$.

When x and N are large a useful approximation for the number of hosts that will receive p parasites when x parasites are distributed at random among N hosts is $\frac{1}{\lfloor p}\left(\frac{x}{N}\right)^p Ne^{-\frac{x}{N}}$ (Poisson series).

ON THE CONTROL OF *ANTESTIA LINEATICOLLIS*, STÅL (HEM., PENTATOM.) ON COFFEE IN KENYA COLONY.

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(Plate IX.)

One of the most serious insect pests of coffee in East Africa is the Pentatomid bug, *Antestia lineaticollis*, Stal. It occurs in Kenya, Uganda and Tanganyika, in which countries it does serious damage. Formerly also, when coffee was an important crop in Nyasaland, a closely related species proved a serious pest in that country.

The two parts of the plant most usually damaged are the bean and the young shoots. When the bean is punctured, it becomes badly discoloured or partly rotten, and if any noticeable percentage is so affected the market value of the crop is seriously lowered.* The feeding of the bug at, or near, the growing point of a shoot may prevent its normal growth, by stimulating at this point the adventitious growth of a number of shoots (Plate ix). This form of damage can be very serious; in bad cases the tree may thus be completely deformed, and it is difficult so to prune the tree as to shape it again when once it has been badly damaged in this manner. Here, the following observations of planters on damage by *Antestia* may be quoted :—

"The trees which were attacked by them are still in an awful state." 11th Sept. 1911.

"After a bad attack we have found the tree appears poisoned right through and takes a long time to recover." 6th April 1918.

"This is the cause of a 30 acre patch of my coffee going in completely last year." 18th June 1919.

"Thirty acres of five-year-old coffee not bearing, undoubtedly through a bad attack of this bug last year." 18th June 1919.

The life-history of the bug and of the two chief species of egg parasites has been described in detail by Anderson,[1] and here I have permission to give the following details from his paper.

The egg-stage lasts from 1 to 2 weeks according to the season of the year; the 1st instar nymph apparently feeds little if at all, and the duration of this stage is about 12 days; the duration of each of the 2nd, 3rd, 4th and 5th nymphal instars is about three weeks. The length of life of the adult female is about 130 days but may be as much as 290 days, and the number of eggs laid may be as high as 485. The average length of life of the male is about 106 days.

The two chief egg parasites are *Telenomus truncativentris*, Dodd, and *Hadronotus antestiae*, Dodd. At least three other species of parasites or hyperparasites have been bred from the eggs, namely *Barycornus* sp., *Aprostocetus* sp., and *Anastatus bifasciatus*, Fonsc.,[2] but at present none of these is of great importance.

Anderson gives the following figures of the percentage of eggs parasitised in collections made from one block of coffee every month from July 1917 to December

* It has been shown by Wallace[10] in Tanganyika that this rotting of the beans is due to a fungus, *Nematospora coryli*, Peglion, the spores of which are inoculated into the coffee "cherry" by this insect.

1918. Of a total of over 10,000 eggs, 78 per cent. were parasitised, 14 per cent. produced *Antestia*, and 8 per cent. did not hatch. The percentage of eggs parasitised varied between 48 per cent. and 93 per cent. The following figures are from collections of eggs made on various coffee estates.

	Per cent. parasitised.	*Per cent. hatching Antestia.*	*Per cent. not hatching.*
(1)	79	7	14
(2)	82½	7	10½
(3)	91	7	2
(4)	46½	52	1½
(5)	86	4½	9½
(6)	84	6½	9½

In no case were these figures based on collections of less than 400 eggs.

During the first years of the importance of *Antestia* as a pest in East Africa, the chief control method employed was hand-picking of the bugs, supplemented in some cases by collection of the eggs and liberation of the parasites obtained from them.

The hand-picking is done either by searching the tree branch by branch ; or by the effective method of smoking the tree from below, which causes the bugs to move along the primaries and down the stem of the plant, where they may be collected. Some slow-burning substance which smokes freely, such as moist cow-dung, carried in an empty petrol tin is used for this purpose. The value of this method is undoubted ; when begun sufficiently early and carefully and systematically carried out, it is nearly always possible to prevent a serious attack by this means ; but the chief drawback is its expense. On a hundred acres of coffee it may be necessary to keep 50 native children working in this way for one or two months or even longer before the numbers of the bug are sensibly reduced. This costs about £25 a month. The number picked varies, of course, according to the intensity of *Antestia* infestation ; when the average number of bugs on a tree is only one or two, the number picked by a child in one day is about 50, and below this number it would seem to be uneconomical to continue hand-picking ; when the average is as high as 50 to a tree, which condition the writer has seen on one occasion, a child will obtain between 500 and 900 a day. When *Antestia* has become so numerous, the attack is most difficult to control by hand-picking, and again is it questionable whether the measure is economical.

The egg-batches, which are usually laid on the undersides of leaves, are difficult to find, and usually about eight out of ten batches are parasitized ; for this reason many planters do not collect them. It is, however, advisable to instruct the labourers to bring in all the egg-batches they happen to find when picking the bugs, afterwards liberating the parasites which emerge and destroying any *Antestia* which hatch.

Contact sprays were also tried when *Antestia* first became epidemic, and one was recommended by Gowdey[3] in Uganda :—

Caustic soda 92 per cent.	4 lb.
Resin	6 lb.
Whale oil soap	10 lb.
Dilute with water to	45 gallons

Also in Kenya the following spray had some success :—

Nicotine sulphate 40 per cent. ...	6½ oz.
Sunlight soap	8 lb.
Water	50 gallons

However, owing to expense and the great difficulties of spraying coffee adequately, contact spraying never became general.

The control method that is now in general use against the bug, which may be called the "poison-bait-spray" method, will be described and examined in some detail, as it seems to be of considerable theoretical importance.

So far as the writer is aware, the first attempt to control this insect, which normally feeds in the usual hemipterous manner by inserting its stylets into the plant and extracting its food therefrom, by means of poison baits, was suggested and made in Kenya in 1914. The method of application which later came into general use, that is, spraying the mixture on the tree, was also suggested at this time. The mixture tried was as follows :—

Paris green	1 lb.
Lime	2 lb.
Cheap sugar	30 lb.
Water	150 gallons

together with juice extracted from ripe coffee berries. These experiments did not appear to have any success and work with poison baits was not continued at that time.

Later Ritchie[4] described preliminary experiments with the poison-bait-spray method begun in Tanganyika in 1923. The formula he adopted for trial was :—

Sodium arsenite	100 grms.
Native sugar	1 kilo
Water	100 litres

and he stated that "evidence is accumulating that a sweetened poison spray can be applied against this pest with considerable effect." Similar experiments were also made in Kenya and Uganda, and now the method is well known and much practised commercially.

The method of application will be described in some detail. A poison bait, most usually consisting of :—

Sodium arsenite...	1 oz.
Jaggery (unrefined sugar)	2½ lb.
Water	4 gallons

is sprayed on the trees so that a light mist falls on the leaves. The spraying machine most usually employed is an ordinary knapsack sprayer. The boy applying the bait walks quickly between the rows of coffee, holding the nozzle of the sprayer in the air, which allows the wind to carry the light mist over the coffee bushes. As the object is to place a large number of small drops of the bait on the tree, other methods of applying it have been suggested. It is said that success has been obtained by dipping bundles of brushwood into the solution and whisking it on the bushes. Though the writer has not tried it in practice, this method would seem to have some disadvantages.

The bait method was apparently used before there was any detailed knowledge of how it acted. That the bugs did feed on the poison was assumed because numbers were afterwards found to be dead on the ground under the sprayed bushes. The following laboratory observations show that the bug is attracted by the bait and that it can suck up the poison from the small drops on the surface of a leaf :—

> Leaf sprayed with poison bait placed in petri dish with two *Antestia* 2nd instar nymphs. One of the nymphs immediately went to a small drop of the sweetened poison and lifted the proboscis into it, staying in this position for some time. The next morning both the nymphs were dead, while others from the same batch of eggs, not having access to the poison, were alive.

In three laboratory trials, the mortality of bugs in cages with coffee shoots sprayed with the poison bait was considerably higher than in cages with coffee shoots sprayed

with plain water ; but is seems evident that some few of the bugs either do not suck the poison or take less than a lethal dose, because a small number were alive even after 7 days access to the poison.

Cages 1, 2, 3 contained coffee shoots in water, which were sprayed with the standard formula (sodium arsenite 1 oz., jaggery 2½ lb., water 4 gallons). Cages C1, C2, C3 contained shoots in water, which were sprayed with plain water. Opposite the first date in the following table is the number of live insects placed in the cage on that day. Opposite subsequent dates is the number of insects which had died during the previous 24 hours. In the first two trials adults and nymphs were used, in the third adults only.

Date	Cage 1	Cage C1
13th December	20 alive	20 alive
16th ,, ...	8 dead	3 dead
17th ,, ...	4 ,,	0 ,,
18th ,, ...	3 ,,	0 ,,
19th ,, ...	3 ,,	0 ,,
20th ,, ...	0 ,,	0 ,,
Total	18 dead 2 alive	3 dead 17 alive

Date	Cage 2	Cage C2
16th December	50 alive	50 alive
17th ,, ...	5 dead	2 dead
18th ,, ...	9 ,,	5 ,,
19th ,, ...	7 ,,	4 ,,
20th ,, ...	10 ,,	5 ,,
21st ,, ...	6 ,,	3 ,,
22nd ,, ...	6 ,,	1 ,,
23rd ,, ...	2 ,,	1 ,,
Total	45 dead 5 alive	21 dead 29 alive

Date	Cage 3	Cage C3
31st December	20 alive	20 alive
1st January	3 dead	1 dead
2nd ,, ...	3 ,,	3 ,,
3rd ,, ...	4 ,,	2 ,,
6th ,, ...	7 ,,	2 ,,
Total	17 dead 3 alive	8 dead 12 alive

Taking the three experiments together it will be seen that after 7 days, of 90 insects having access to the poison, 80 were dead and 10 alive ; while of 90 insects not having access to poison, 32 were dead and 58 alive. In these trials there was a fairly high mortality in the controls, because *Antestia* did not take happily to the confinement.

The application of a solution of sodium arsenite on the leaves causes some scorching, but this is seldom important in practice if the application is carefully made, because the design is to allow only a fine mist to fall on each tree, and the small burned spots on a few leaves are negligible.

The total cost of this measure is very small. It works out in practice at about one shilling an acre for one application.

In Tanganyika Ritchie[5] says "Considerable success has attended the use of the poison syrup against *Antestia*. The spray has been adopted as the standard control of the coffee bug throughout the coffee areas. . . . The former ineffectual and expensive method of hand-picking the bugs has been entirely given up." In Kenya, however, where it has now been used commercially for several years, planters have not found it invariably successful. It is considered useful to give here some of their own views as to its efficacy.

"½-oz. sodium arsenite certainly has diminished the number of *Antestia*."

"Arsenite has proved very deadly on all insects except *Antestia*." 9th June 1926.

"Arsenite bait applied three times and *Antestia* increasing very rapidly." 7th April 1926.

"Slight general attack which remains practically the same in spite of hand-picking and spraying." September 1929.

"Spraying has not proved effective."

"The whole plantation was sprayed twice. . . . Never has the outbreak been so serious as subsequent to these precautions which were never taken before." 11th June 1928.

Another planter states that he finds the spray most satisfactory. Whenever the bugs begin to increase the whole estate is sprayed, and he has had no trouble since he adopted this practice (verbal communication, 1930).

It appeared to the writer that the unsatisfactory results might possibly be due, at least in part, to poisoning of the egg parasites of the bug. This seemed not unlikely because of the high percentage of parasitism and the certainty that this is an important factor in the natural limitation of the bug. It has been pointed out by Dry[6] that the data available are "too few for us to be able to correlate the occurrence and subsidence of outbreaks of *Antestia* with parasite conditions." He found that in collections of eggs made during outbreaks of *Antestia* the percentages of parasitised eggs were sometimes as low as 37 per cent. and sometimes as high as 87 per cent.; and on the other hand on plantations where *Antestia* had never been serious, he found the parasites sometimes present in force, 86 per cent. of the *Antestia* eggs being parasitised on one such plantation.

On the supposition then that the parasites are killed, this fluctuation in their intensity would seem to allow for varying results following application of the poison. That varying results are caused in practice by the killing of the parasites could only be proved by the collection of large numbers of eggs, and the determination of the percentage parasitised at different times during epidemic attacks of *Antestia*, and before and after spraying. Time did not permit of this being done, nor indeed were there any attacks during the course of this work of sufficient intensity to be likely to yield satisfactory figures; but it was decided to determine in the laboratory whether the parasites were attracted by the sweetened arsenic bait, and also to ascertain what insects were killed by it in the field, following an ordinary commercial application.

A number of trials were made with parasites in the laboratory. Coffee leaves sprayed with the ordinary poison bait were placed in petri dishes with parasites, and leaves sprayed with a similar, but unpoisoned, sugar solution were placed similarly with parasites as controls. The parasites in almost every case rapidly found the drops of sugar on the leaves, and both in the poisoned and unpoisoned dishes immediately began to imbibe it.

The results are given in the following table. For convenience of recording, each parasite is given an index number, and in the second column are the index numbers of parasites placed with the poison bait, while in the third column are the index numbers of parasites placed with unpoisoned sugar. The first date indicates the beginning of the experiment, and opposite the second and subsequent dates the condition of the

parasites is recorded. In each test parasites bred from the same batch of *Antestia* eggs were used in sprayed and control dishes.

Date and time	Parasites with poison bait	Parasites with unpoisoned sugar solution
5. xii.	1, 2, 3	4, 5
6. xii.	All dead	Both alive
7. xii.	4, 6	5
8. xii.	Both dead	Alive
19. xii.		Alive
21. xii., 3 p.m. ...	7, 8, 9, 10, 11, 12, 13	14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24
21. xii., 6 p.m. ...	Three dead	All alive
22. xii., 10 a.m. ...	All dead	,,
21. xii.	25, 26, 27	28, 29, 30
22. xii.	All dead	All alive
22. xii.	14, 21	15, 16, 22, 23, 24
23. xii.	Both dead	All alive
27. xii., 2 p.m. ...	31, 32	33, 34, 35
27. xii., 9 p.m. ...	Both dead	All alive
29. xii.		,,

Thus, of 19 parasites having access to poison bait, 19 died within one day (and some died within 3 hours); and of 19 parasites with access to unpoisoned sugar, 19 were still alive at the end of one day's interval. This shows that the parasites are strongly attracted to the poison and rapidly succumb to it.

In the field the investigation was broadened to attempt to determine the total effect of this poison spray on the fauna of the plantation. This was considered of importance because there seemed to be no recorded information on this point, and there was a possibility that other valuable parasites as well as those of *Antestia* might be killed, and on the other hand other injurious insects besides *Antestia* might also be poisoned in large numbers.

A cloth sheet measuring 9 ft. by 9 ft. was slit from the middle of one side to the middle of the sheet, and placed under a coffee tree with the trunk in the middle of the sheet, and the slit was then sewn up. A narrow border consisting of tree-banding grease was then applied, and the tree sprayed in the usual manner for the control of *Antestia*. The intention was to have a fairly complete list of the insects poisoned, by examining and counting those which dropped on the sheet. This proved not very successful because, owing to leaves blowing on to the sheet and bridging the surrounding grease band, a rather large number of ants got on the sheet from the soil, and probably a large number of insects were blown off the sheet. The results are, however, given in Column A of the following table. No control sheet was used in this case.

A very satisfactory method was afterwards devised. This was a sheet similar to the one described, but without the grease, and with sides three feet high of the same material (known in this country as "amerikani"). The sides were held up by posts at the four corners. This constituted a sort of basin under and around the tree which, when sewn up, has no holes or interstices either for the escape of insects fallen from the tree, or for the entry of insects from the soil, and it was too deep for insects to be blown out of it.

The number of insects obtained in such a sheet from a tree sprayed with the bait is given in column B. And in column C is the number obtained in a similar sheet under a tree which was not sprayed. When the family of the insect was readily recognised, this was recorded; in a few cases the genus or species happened to be known, otherwise the order alone is given, as with such a very large number of insects time did not permit any detailed examination. In cases where the insects were of particular interest, they were retained for identification and their collection index number is given (*e.g.*, C67, P475, etc.).

Animals obtained	A	B	C
Total animals	586	1,392	72
Total Arthropoda	583	1,391	71
Total Insecta	576	1,363	65
DIPTERA Total	268	896	7
Mycetophilidae	29 (3 spp.)	25 (4 spp.)	
Bibionidae	5	7	
Tipulidae	3 (2 spp.)	8	
Culicidae	2	—	
Empidae	—	5	
Syrphidae	6 (2 spp.)	6	
Trypetidae	2	18 (3 spp.)	
Muscidae	10 (4 spp.)	16 (several species)	
Sarcophagidae	8 (3 spp.)	6	
C 67	3	3	
P475	5	—	
T295	78	10	
Larva	1	—	
Other	116 (many species)	792 (many species)	
HYMENOPTERA Total	111	129	14
Ichneumonoidea Total	30	13	
T270, parasite of *Thliptoceras*	8	—	
Apanteles coffea, Wilkn., parasite of *Thliptoceras* ...	4	1	
Other	18 (several species)	12 (several species)	
Parasites, chiefly Chalcidoidea and Proctotrupoidea Total	26	94	7
Parasite of *Saissetia subhemisphaerica*	4	—	
Egg parasite of *Antestia* ...	—	6	
Other	22 (several species)	88 (40–50 spp.)	
Ants	52 (5 spp.)	8	7
Other	3	14	
COLEOPTERA Total	37	34	3
Staphylinidae	2 (2 spp.)	14 (2 spp.)	3
Melolonthidae	3	—	
Halticinae	6	—	
Chrysomelidae	—	1	
Stephanoderes hampei... ...	1 (alive)	—	
Systates sp.	2	2	
Gonocephalum sp.	1	—	
Scymnus sp.	3	1	
Larva	—	4	
P481	10	—	
Other	9 (several spp.)	12 (several spp.)	

Animals obtained	A	B	C
RHYNCHOTA Total	16	35	8
Capsidae Total	8	17	2
Lygus simonyi	6	12	2
T325	—	5	
Other	2	—	
Anthocoridae		3	
Cercopidae	4 (2 spp.)	3	3 (2 spp).
Psyllidae	—	—	1
Ploiariodes sp.	—	2	
Toxoptera aurantii	2	6	2
Ceroplastes destructor	1	—	
Lecanium hesperidum ...	1	—	
Saissetia oleae	—	1	
Saissetia nigra	—	1	
Other	—	2	
LEPIDOPTERA Total	8	35	
Noctuidae	3 (3 spp.)	20 (several spp.)	
Thliptoceras octoguttalis ...	—	1	
Eucosma nereidopa	—	1	
Larva	1	—	
Other	4 (3 spp.)	13 (several spp.)	
PSOCOPTERA Total	82	187	21
Ectopsocus briggsi	82	185	21
Other	—	2 (2 spp.)	
COLLEMBOLA Total	49	4 (3 spp.)	11 (3 spp.)
THYSANOPTERA Total		33	
T333	—	16	
Other	—	17 (4 spp.)	
ISOPTERA Total	2		
NEUROPTERA Total	3	8	1
Hemerobiidae	2	6	1
Chrysopidae	1	2	
TRICHOPTERA Total		2	
ARACHNIDA Total	7	28	6
Spiders	6 (4 spp.)	27 (several spp.)	6
Mite	—	1	
Tick	1	—	
ANNELIDA Total		1	
GASTROPODA Total	3		1

No *Antestia* was obtained in either of the sheets, but the experiment had to be made when this insect was in small numbers; in the block in which sheet A was put down (20–23 Oct.) the average number to a tree obtained by hand-picking was less than 2; and in the case of sheet B (16–20 Dec.) the average was between 4 and 5. Thus it cannot be certain that *Antestia* was present on the trees sprayed.

With the fairly complete inventory of insects poisoned by the spray, it is possible to discuss whether any effects other than the control of *Antestia* are likely to follow its application.

It will be seen that 56 Hymenopterous parasites were obtained on Sheet A, and 107 on Sheet B. A small number of these were egg parasites of *Antestia*, and in addition parasites of *Thliptoceras octoguttalis*, the Coffee Berry Borer Moth, and *Saissetia subhemisphaerica*, the Brown Scale, were recognised. Most of the rest of these insects were probably parasitic on insects injurious to coffee, though it is possible that some of them were hyperparasites. It is known that parasites of *Thliptoceras* are themselves parasitised, and in all probability the same occurs with some of the scale parasites. The adult *Antestia* are parasitised by a Hymenopteron which the writer has obtained in large numbers. This insect (T334) has not yet been identified and its value in controlling *Antestia* has not yet been determined. On the whole, however, this effect of the spray in attracting and killing a large number of various Hymenopterous parasites must be considered decidedly disadvantageous, and evidence tending to show that serious results may follow this destruction of parasites will be adduced later.

The majority of the insects are Diptera, and most of these are neither beneficial nor injurious to coffee. The SYRPHIDAE, of which a very few were obtained, feed in the larval stage on mealybugs and the coffee Aphid and are beneficial. The only other flies known to be beneficial are two unidentified parasites of the adult *Antestia* which the writer has bred, neither of these was present in the sheet. One of these may be the Tachinid, *Epineura rubens*, Vill., mentioned by Wilkinson.[7]

Of the Coleoptera obtained, the leaf-eating weevil *Systates* sp. is a very minor pest, and the two examples on each sheet probably took enough poison to kill them when eating leaves. The presence of the Coccinellid *Scymnus* may have been accidental. The other beetles are mostly innocuous.

Of the Rhynchota, doubtless the spray has nothing to do with the presence of Coccids and Aphids on the sheets. *Lygus simonyi*, Reut., the Capsid which causes abortion of the coffee flowers, was present on the trees in fairly large numbers at the time of the experiment. It has been shown in the laboratory that this Capsid will on occasions suck a sugar solution in a similar manner to *Antestia*, and it is probable that the few that fell down in this case were killed by sucking the poison. Although *Lygus* will not usually take the sugar solution if coffee buds are available, the fact that it can do so, in addition to the fact that *Antestia* may be controlled by this means suggests that stomach-poisons for the control of insects which normally feed by sucking the plant internally deserve further investigation.

The Lepidoptera found probably include the adults of some leaf-eating caterpillars. None of these was identified for certain, but several species of NOCTUIDAE have been bred from larvae feeding on coffee foliage.

Of the Psocoptera, *Ectopsocus briggsi* was shown by Kirkpatrick[8] to be a valuable predator of mealybug ; it is in addition a fairly omnivorous scavenger, and doubtless took the poisoned sugar when available. The killing of a large number of Psocids is a serious disadvantage.

The Collembola on Sheet A may have jumped on from the soil, because only four were present in Sheet B, although it should be mentioned that at times they are present on the trees in large numbers.

Among the five species of Thysanoptera obtained on Sheet B, *Diarthrothrips coffeae*, the coffee pest, was not present. At least one of the species is carnivorous, and this one may possibly have taken the poison.

The rest of the insects and other animals are of little importance.

On the whole, excepting the *Antestia* itself, for which it is applied, it appears from these figures that the poison bait kills more beneficial than destructive insects.

Owing to the destruction of Hymenopterous parasites, it would be expected that the spraying would cause an increase of those insects, such as certain COCCIDAE,

which are known to be usually kept within reasonable limits by them. In this connection the following observations are significant.

Two adjacent estates, both subject to attack by *Antestia*, employed different methods of control. On Estate A, oft repeated sprayings with the poison bait for 18 months kept the bug in check, and on the other the same object was attained during the same period by hand-picking the bugs. On Estate A, after 18 months of the treatment, several species of COCCIDAE were present generally throughout, and were especially numerous in one block in the centre of the estate. On Estate B at the same time, scale-insects were few and were nowhere more numerous than they were generally throughout. The centre block was examined in both estates. Twenty trees were selected at random and ten shoots examined on each tree, and the results are seen in the following table.

Insect	Estate A		Estate B	
	Number of trees on which insect was found	Number of shoots on which insect was found	Number of trees on which insect was found	Number of shoots on which insect was found
COCCIDAE—				
Pseudococcus lilacinus ...	3	17	1	1
Lecanium africanum ...	2	2	none	none
Lecanium hesperidum ...	6	9	1	1
Saissetia oleae	20	130	2	2
Saissetia nigra	12	16	2	2
S. subhemisphaerica ...	3	4	1	1
Ceroplastes destructor ...	18	50	1	1
Ceroplastes rubens ...	1	1	none	none
Pulvinaria psidii	1	1	none	none
Cerococcus hibisci	1	1	none	none
Icerya nigroareolata ...	1	1	1	1
APHIDAE—				
Toxoptera aurantii ...	3	3	none	none
Total	20	172	8	9

On Estate A, 120 shoots were attacked by one species of scale, 41 shoots had two species on each, and 11 shoots had three species. On Estate B no shoot had more than one species.

That this striking difference was due to the effect of the spray could only have been proved by continued breedings and counts of the scale parasites on each estate, and time did not permit of this work, but there was no important difference between the two estates except the different measures used for *Antestia* control.

Still further evidence pointing to the same conclusion, that the destruction of parasites may allow a pest to become serious, when before it was present only in small numbers, was seen on Estate A in 1931. Several repeated sprayings were made in December 1930, and by February 1931 there was a very serious attack of Leaf Miner Moth (*Leucoptera coffeella*) on the estate, which caused the almost complete defoliation of 8 or 10 acres, and was very severe over a much larger area. This moth is heavily parasitised in the larval and pupal stages (Box[9]), and though present probably on every estate in the country, it is very rarely of any consequence on established coffee, though it sometimes does damage in nursery beds. This was the first attack which caused any appreciable loss that the writer had seen in visits to a large number of estates in different districts. Here it was estimated to have reduced the crop on the 8 to 10 acres by at least 75 per cent., and the defoliation may have a deleterious

effect on the trees for some time. On the neighbouring Estate B this moth was present in no greater numbers than usual.

With the facts here adduced, it is possible to decide on the times and conditions when this spraying against *Antestia* is likely to be most effective and least dangerous. It has been the general experience that, in the wetter districts, it is a less valuable measure than in drier districts. It is clear that if rain falls, say 24 hours after the application, washing the spray off the tree, the parasites are likely all to have been killed and the *Antestia* not, and the spraying will therefore fail to achieve its purpose, the *Antestia* increasing rapidly.

The year 1930 was one of exceptionally heavy and consistent rainfall, and on Estate A it was noted that very few of the many applications of the bait throughout the year remained on the tree for a longer period than 3 days without being washed off by rain, and the *Antestia* continued to be serious on this estate throughout the year, and several times it was necessary to supplement the spraying by hand-picking.

If a dry spell allows the spray to remain on the tree for 4 or 5 days the best results are achieved, and if such a dry period can be fairly certainly predicted, the application of the spray can be recommended. In showery or unsettled weather the spray may do more harm than good and cannot be recommended.

Again, if one or two sprayings are not effective in controlling the bugs, it may well be more advisable to alternate with this measure an intensive hand-picking, returning again to spraying if desired; this may prevent a progressive depletion of the parasite population of the estate, and render a serious attack by another pest unlikely.

It may be possible to devise other means of applying a bait which will be more satisfactory in the wet districts. Should opportunity permit, it is hoped to experiment with other methods and to include an account of these in a second paper. At present, however, in wet weather, it seems better to rely on hand-picking the bugs and egg-clusters and releasing the parasites.

Summary.

1. The damage done to coffee by *Antestia lineaticollis*, Stål, is shortly described and notes on its life-history are given.

2. It is parasitised in the egg-stage by two important species of Proctotrupoid parasites, the percentage of parasitism usually varying around 80 per cent. and in one case quoted being as high as 91 per cent.

3. Of the control measures employed, contact-spraying has not proved satisfactory; hand-picking of the bugs and egg-clusters and liberation of the parasites are widely practised and, though troublesome and expensive, are of considerable value; another method of value and widespread adoption has been called the "poison-bait-spray" method. This is described in detail; it consists in the application of a stomach-poison in the form of a solution of sodium arsenite and sugar to the tree by spraying. Laboratory observations show that the insect imbibes the poisoned solution by lifting the proboscis into small drops on the leaf surface, and there is a definite kill due to the use of this poison.

4. In Kenya, its use commercially, while often of proved value, has not been invariably successful. Experiments showed that the egg parasites of the bug were strongly attracted by the poison spray and quickly died after feeding on it. It is suggested that this may be the cause of some of the unsuccessful results.

5. A determination of the effect of the spray on the fauna of the coffee was made. From one tree 1,392 animals, of which 1,363 were insects, were obtained. These were mainly flies (896), but 107 parasitic Hymenoptera were also killed, including parasites of *Antestia*, *Thliptoceras*, and certain Coccids. It appears that, excluding the *Antestia* itself, the spray causes the death of more beneficial than injurious insects.

6. On an estate where this spraying had been done fairly frequently for 18 months, the number of individuals and species of COCCIDAE on the coffee was considerably higher than on a neighbouring estate where the *Antestia* had been controlled by hand-picking.

7. A serious attack of Leaf Miner Moth (*Leucoptera coffeella*) also occurred on this estate, following several sprayings with the poison bait. This moth is parasitised in the larval and pupal stages and, though generally present in Kenya, is extremely rarely of any consequence.

8. It is suggested that the use of such poison baits against sucking insects offers a valuable field for further investigation. Similar control measures, which run counter to the simple division of " contact-sprays for sucking-insects " and " stomach poisons for biting insects " may prove to be of more general application.

9. Some observations are made on the most suitable conditions for spraying.

My acknowledgments are due to the Senior Entomologist, Mr. T. J. Anderson, for allowing me to quote from his paper and for kindly reading the manuscript.

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Coffee branch attacked by *Antestia*, showing development of adventitious shoots.

CHITINISATION OF PARASITES IN MOSQUITOS.

By S. L. Brug,

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(Plate X.)

Various instances of the formation of a chitinous capsule around parasites in mosquitos have been described in literature. Worms as well as Protozoa, Hyphomycetes and bacilli have been seen encapsuled in this way.

Manson-Bahr (1912, p. 25 and 1921, p. 595) described larvae of *Filaria bancrofti* in *Aëdes* (*Stegomyia*) *variegatus* enclosed in a chitinous capsule like mummies in their coffins. Many times he met with these structures in sections of the mosquitos. According to this author dead worms were most frequently isolated in this way a similar phenomenon was observed by Fülleborn (1929, p. 1119) in the Malpighian tubes of *Aëdes* (*Stegomyia*) *fasciata* infected with the larvae of *Filaria repens*. This author also states that dead worms are subject to chitinous encapsulation. Apparently the same structures have been observed by Noë (1900) in the Malpighian tubes of mosquitos infested by the larvae of *Filaria immitis*. I have been unable to consult Noë's original paper, but from the references to it by Fülleborn (1929) and Sambon (1902), I gather that Noë considered these structures to be products of degeneration ("brown degeneration") of the worms. Sambon (1902) discussing Noë's paper, and in the discussion of a paper by Low (1908) supposes that the brown capsules seen by Noë are secondary parasites of the worm (comparable with the *Nosema* of silkworms) and suggests that they may account for the limitation in the distribution of *F. bancrofti*.

Brug (1916) offered a solution to the problem of the nature of the "black spores" as found in the *Proteosoma* cysts in the mid-gut of *Culex pipiens* by considering them to be chitinous corpuscles formed by the mosquito as a reaction to the parasite's presence. The suggestion that black spores are chitinous structures was confirmed by the researches of Walch (1921) and Mayne (1929). The latter author laid particular stress upon the relationship of the black spores to the tracheal tubes of the mosquitos. He found the "spores" actually inside the lumen of these tubes. Moreover, he found as did Walch, black spores in mosquitos quite independently of a malarial infection.

Structures quite similar to black spores were found by Grassi (1903) in *Anopheles* infected with myxosporidian parasites. According to this author some spores of the parasite were subject to brown degeneration. From his figures it is apparent that the spores showed a capsule of a dark brown substance. I think it very probable that Grassi's observation is another instance of chitinous encapsulation of a parasite.

Walch (1921) described other cases of chitinisation of parasites of mosquitos. He observed a hyphomycete that had pierced the wall of the oesophagus and that was coffined in chitin on having reached the thoracic cavity. He also saw groups of bacteria, as well as single bacteria, enclosed in a chitinous capsule.

Marshall (1929) made the interesting observation that at the points where mites are attached to mosquitos—*Aëdes* (*Aëdes*) *cinereus* and *Aëdes* (*Ochlerotatus*) *annulipes*—chitinous tubes are produced toward the interior of the host. These chitinous formations may be considered as analogues of the "tongue" of *Leptus autumnalis*. This "tongue" is a tubular organ attached to the mouth-parts of the mite, when it is detached from a vertebrate host, but absent in the free-living mite. The question of

the " tongue " of *Leptus* puzzled entomologists until André (1927) explained that it is no part of the mite, but a product of the reaction of its host, produced by an injection of a digestive fluid by the mite. Marshall's observations are strongly in favour of André's thesis that the tongue is part of the host, not of the mite. For the " tongue " of the mites preying on mosquitos consists of chitin, whereas that of *Leptus*, preying on vertebrates, is soluble in caustic potash.

I can now add another instance of chitinisation of a protozoan parasite in a mosquito. Although I am unable to name the parasite, I think that from a general point of view the observation is worth recording. The parasites were seen in sections of a mosquito (*Taeniorhynchus* (*Mansonioides*) *annulatus*) that had been artificially infected with *Microfilaria malayi*. In the sections " ripe " larvae of the worm were present, but I failed to detect any connection between the worms and the protozoan parasites (in the sections of about 40 other mosquitos, partly *T.* (*M.*) *annulatus* and partly *T.* (*M.*) *annulipes*, no protozoa were seen). The protozoan was found in the neck, in the thorax and in the base of the abdomen of the gnat (the remainder of the abdomen had been cut off in order to allow the fixing fluids to penetrate freely), but in the head they were absent. In the thorax it was seen between the muscles, and around the foremost part of the midgut as well as under the skin. In Plate x, fig. 1 three parasites may be seen (2, 3, 4). Fig. 2 represents the foremost parasite at a larger magnification ; it looks like the section of a dendritically ramified structure evenly stuffed with nuclei and suggests the schizogonic stage of some protozoan. Similar formations were seen in many places in the mosquito's thorax, differing in size considerably, but all showing the same structure. In fig. 3 a small section of a parasite, perhaps an offshoot of such a one as depicted in fig. 2, is drawn at a still larger magnification in order to show the structure of the nuclei.

The most remarkable structure is seen in fig. 4. Its colour varies from dark brown to yellowish brown. Apparently it is a piece of chitin, situated at a place where in a normal mosquito there ought not to be any chitin. It cannot be a piece of the cuticula transported by the microtome knife, for if it was, the section would have been badly damaged. It shows holes just large enough to admit the rami of such a parasite as shown in fig. 2. In most of these holes a varying number of nuclei may be seen, resembling those in parasite 2 but less in number. I think it may be safely concluded that this figure represents a parasite in the process of being enclosed in chitin. In the upper part of the figure many nuclei of the parasite have already been resorbed, in the lower part there is retained more of the structure of the parasite.

About the nature of the parasite I do not dare to offer a definite opinion. It *might be* the plasmodium stage of a mycetozoan, but in the absence of any other stage a definite diagnosis is well nigh impossible. Parasitism of Mycetozoa in insects (beetles) has been described by Léger & Hesse (1905) in *Otiorrhynchus fuscipes* and by Léger (1908) in *Scaurus tristis*.

From a pathological point of view the chitinisation of parasites can best be compared with the calcifying of parasites as observed in human pathology. Walch (1921) pointed out that in both cases the parasites are enclosed in substances that in normal circumstances form the skeleton, calcium carbonate in the vertebrate and chitin in the insect.

The chitinisation can hardly be considered as a means of defence against living parasites. So far as we know, malarial parasites are hardly pathogenic for their insect hosts ; the latter can stand even the heaviest infections without showing any apparent symptom of disease, and in this case there is not the slightest occasion for the mosquito to " defend " itself against this parasite as there is no " attack." On the other hand, it is well known that a heavy filarial infection can greatly damage the mosquito and, at least in captivity, even kill it. If in this case the chitinous encapsulation of the worm might be considered as a means of defence, it must be granted that it is not a very successful one. For most of the parasites escape encapsulation, which

occurs fairly rarely. In Bahr's figure (1912, p. 25) we see in a section of a mosquito one filaria enclosed in chitin side by side with many lying free between the muscles and looking quite healthy. We do not know whether the Myxosporidium, observed by Grassi or the protozoan that I saw myself did in any way endanger the mosquito's life. But at any rate in these cases, just as in the case of filarial parasitism, only a small part of the parasites were chitinised.

I have been unable to make out on what grounds Manson-Bahr (1921) and Fülleborn (1929) came to the conclusion that only dead filariae are enclosed in chitin. But the fact that usually only part of the parasites undergo this process is certainly in favour of their thesis. Apparently there are two kinds of parasites, one liable to be chitinised and one not so; the simplest hypothesis to explain this fact is, that the two kinds of parasites are the dead ones and the living ones. A subsequent hypothesis might be worded thus: The chitinisation of parasites in the mosquito is a means by which the host prevents the resorption of their dead bodies.

The formation of chitinous tubes as a result of the mites' bites, inflicted on mosquitos, as observed by Marshall & Staley (1929) might be explained teleologically in a similar way; it might be considered as a means of preventing the resorption of the toxic products injected by the mite.

Formation of chitin in the insect body can take place only with the help of ectodermal epithelium. Inside the insect this tissue is to be found not only in the fore gut and hind gut, but also practically everywhere between the organs in the ramifications of the tracheal tubes. So it is not to be wondered that Mayne (1929) found a close connection between the chitinous corpuscles, generally known as "black spores," and the tracheal tubes and concluded that these corpuscles "appear to be chitinous thickenings of the tracheal tubes." It must be remembered that Mayne found black spores not only in malaria-infested mosquitos, but also in laboratory bred ones and in house-flies. It might be reserved for further research to investigate whether in the latter cases parasitism (bacteria aspirated into tracheal tubes, for instance) plays a rôle in the formation of these black spores.

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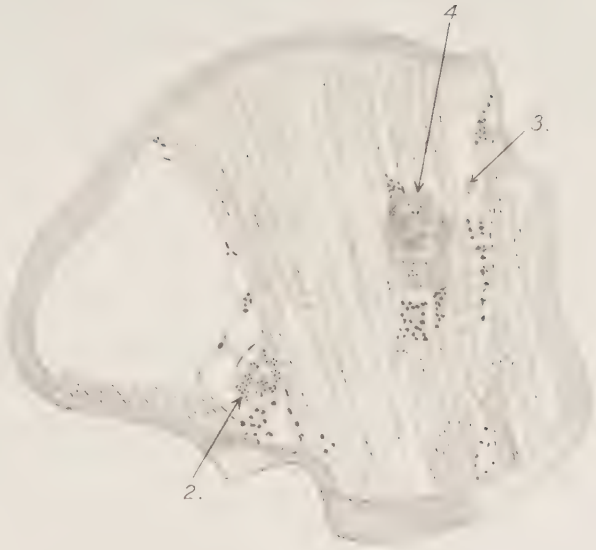


Fig. 1. (×71).



Fig. 2. (×717).

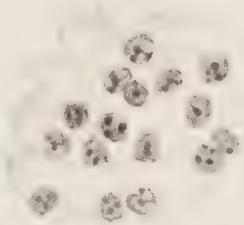


Fig. 3. (×1875).



Fig. 4. (×375).

Chitinisation in mosquitos due to parasites.

A REMARKABLE MALFORMATION IN THE MALE HYPOPYGIUM OF *AËDES (STEGOMYIA) ALBOPICTUS*, SKUSE.

By J. Bonne Wepster.

The male of which the peculiar hypopygium is shown in fig. 1 was bred from a lot of eggs received in March 1931 from Prof. Snijders (at that time in Medan, Deli, East Coast of Sumatra). Other males which had hatched from the same eggs were examined, but they had a normal hypopygium.

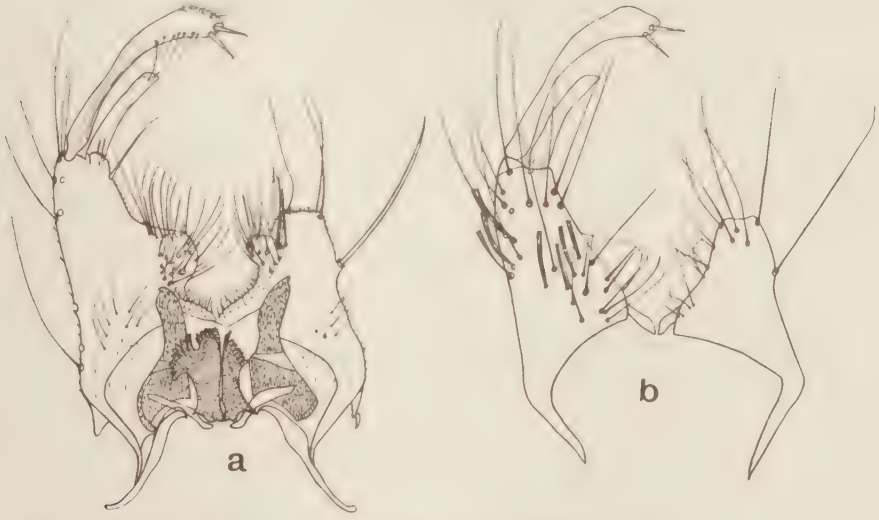


Fig. 1. *Aëdes albopictus*, Skuse, malformed hypopygium of male : *a*, ventral view (after torsion) ; *b*, dorsal view (after torsion).

One side-piece in this malformation is devoid of a clasper, shortened, and bears no scales ; a very long lateral subapical hair is present, slightly differing in ventral and dorsal view. The basal lobe is different from that of the normal side-piece. Basal plates and parameres are normal, as are also the tenth sternites. Comparing the other side-piece with the corresponding structure in fig 2, which was drawn from a normal hypopygium of *Aëdes albopictus*, it agrees with this so far as the *shape* of the side-piece is concerned. There are, however, two claspers, both abnormal. One is small and bears no spine, the other one is of normal size and has two spines. There is no question that perhaps one of the two claspers has fallen off from the other side-piece and that its present position is just the chance position of a clasper detached from its original place. I did the staining and mounting of the hypopygium myself and noticed the malformation as soon as the hypopygium came out of the caustic potash. If the clasper was broken off and just lying loose at the apex of the normal side-piece its position certainly would have shifted again while the hypopygium was passed from one liquid to another.

A striking feature also occurs in the mesosome, of which one half is distinctly double, the other normal.

The malformation is only present in the appendages of the ninth segment (side-pieces) and the chitinizations of the genital tube (mesosome). The tenth (anal) segment is normal.



Fig. 2. *Aëdes albopictus*, Skuse, normal hypopygium.

The imago does not differ in any other way from a normal specimen.

THE NATURAL CONTROL OF THE SHEEP BLOWFLY, *LUCILIA SERICATA*, MEIGEN.

By George Salt, D.Sc., F.E.S.,

Imperial Institute of Entomology.

This paper is my report of a year's work on the sheep blowfly problem at the Farnham House Laboratory of the Imperial Institute of Entomology. The investigation had a two-fold aim. Its immediate object was the development of a satisfactory large-scale method of rearing *Alysia manducator*, and practical results in the form of shipments of the parasite were required. Its ulterior purpose was the accumulation of exact quantitative data on the interaction of a parasite and its host.

The satisfaction of the second purpose entailed careful studies of the reproductive rates of the host and its parasite under known conditions. I commenced, naturally, with the host and in the following pages will be found a fairly complete account of the reproduction of *Lucilia sericata*. Unfortunately, before my study of the host could be completed to my own satisfaction and before the study of the parasite was even well begun, the supply of *Alysia* exceeded the demand and the project was dropped. The general information I hoped to obtain on the interrelations of parasites and hosts, therefore, is not yet forthcoming.

Technique.

My technique was developed with two particular ends in view ; first, that the environmental conditions should be known and capable of duplication ; second, that it should be possible at all stages to determine exactly the number of individuals present.

The adult flies were kept in a greenhouse where the daily range of temperature fell between 18° and 28°C. Temperature and humidity were recorded by a thermo-hygrograph beside the cages but were not controlled, except during the winter, when the temperature was maintained above 18°C. The stock for each generation consisted of twenty-five males and twenty-five females in a cage about twelve inches each way (illustrated in Thompson, 1930, pl. iv, fig. 2). Isolated pairs of flies were kept in simple jar cages (*ibid.*, pl. iii. fig. 2). Sugar fastened with paraffin wax to pieces of cork ; split raisins pinned to the cork ; and a small dish of meat were provided as food. A pad made of cotton-wool wrapped in cloth and contained in a glass dish served as a source of water. In very hot weather when, perhaps owing to the low relative humidity, the flies are apt to damage their wings, water was occasionally splashed through the gauze sides of the larger cages and the blotting-paper floors of the jar cages were kept moist.

It should be remarked, in corroboration of Cousin (1929), that a protein, perhaps a meat, diet is necessary for the development of eggs in the female ovaries. Of nine virgin females emerging within a few hours of each other, five were placed in a jar cage with water, sugar, and raisins ; four in another cage with water, sugar, raisins, and a small jar of meat. On the ninth day eight of these females were dissected. The ovaries of the four provided with meat were packed with fully developed eggs ; those of four without meat were totally undeveloped. The fifth female that had been deprived of meat was then provided with a small amount and a male, which itself had lived twelve days on a carbohydrate diet, was placed with it. On the fifteenth day a batch of eggs was laid which were completely fertile.

Light is also essential to normal reproduction. Adult flies kept in dim artificial light will not oviposit, and under quite strong artificial light many of the eggs laid are sterile. I think this is largely due to the failure of the flies to mate normally. As my stocks were kept in a greenhouse in sunlight no lighting difficulties were experienced.

Eggs for stock cultures were placed directly on the meat in which it was intended to rear them, but for experimental work they were always first separated and counted. Throughout their manipulation blowfly eggs must be kept wet or they will stick to anything they touch and the chorion may be torn. In my experiments eggs were first wetted with clean water and then carefully separated on the wet surface of a piece of gristle. They were then removed in groups of ten to a drop of water on a glass cover-slip. When five groups had been arranged on one cover-slip it was put under the low power of a dissecting microscope and the number checked. The excess water was

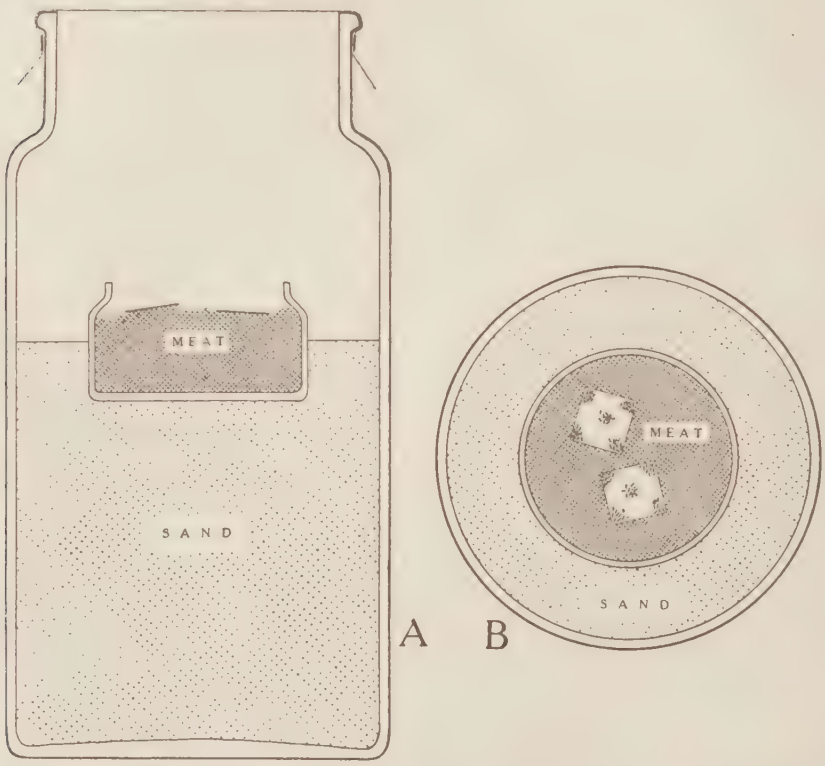


Fig. 1. The arrangement of containers and materials used in rearing larvae of *Lucilia sericata*, Meigen: *a*, median vertical section; *b*, seen from above.

then removed with a bit of blotting-paper and the cover-slip placed on the surface of the meat. The young larvae crawl from the cover-slip to the meat. When hatching is complete the cover-slip may be removed and the number of eggs that failed to hatch may readily be counted among the flattened skins of the hatched eggs. The egg-stage, at 22°C., lasts only 20 hours, so that counting must be done soon after the eggs are laid.

Larvae were reared on a standard medium of minced lean beef, which is not only more homogeneous than pieces of meat but also may be more easily teased apart if it is

necessary to search for the larvae in it. About fifty grams of this food, ample for two or three hundred larvae, was placed in a glass dish about 8 cm. in diameter and 4 cm. deep. This dish was firmly embedded in the surface of clean, dry, sifted sand placed, to a depth of about 15 cm., in a large confectionery jar (fig. 1). The jar was covered with a cloth top held in place by an elastic band and was kept in an incubator at 22°C.

The larvae leave the meat when they are fully fed (on the seventh day at 22°C.) and, after crawling about the surface of the sand for some hours, enter it. The full-grown larvae may be counted as soon as they have left the meat, but they should immediately be returned to the sand for pupation or a diapause may be induced. Pupation normally takes place about the tenth and eleventh days. The puparia were obtained on the fifteenth day by sifting the sand and were placed in tins or isolated in vials for emergence, which occurs, at 22 C., on the twentieth or twenty-first day after the eggs were laid. The emerged flies may be lightly etherized if it is desired to examine them closely before breeding, but they should not be exposed to chloroform, from which they do not seem to recover normally.

The Potential Reproductive Rate of Lucilia sericata.

Kept under the conditions described above, adults of *Lucilia sericata* may live for over three months. The average duration of life of my first and third generation stocks (50 males and 50 females) was 41·0 days for the males and 55·6 days for the females, with maxima of 68 and 104 days respectively.

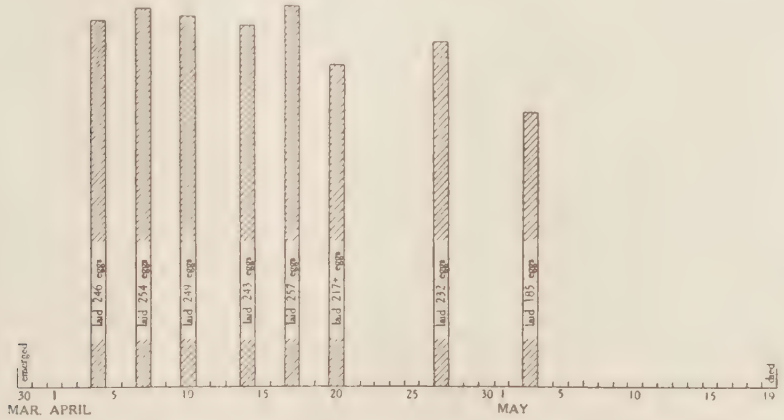


Fig. 2. Graphic representation of the reproductive activity of a female *L. sericata*.

The reproductive period of the male is at least a month and of the female about two months. No attempt was made to determine how long males were able to mate, but I observed copulation in one case when both flies, brother and sister, were 31 days old. The eggs are not laid all at once or continuously, from day to day, but in batches of two to three hundred laid at intervals of three or four days. A typical performance is illustrated in figure 2. Eggs were usually first laid in my cages on the seventh day, but sometimes as early as the fifth day after emergence. Fertile eggs were obtained from a female 66 days old. The oldest ovipositing female observed was one which laid 202 eggs on her 91st day but these were all sterile.

In captivity, with meat always available, females of *Lucilia sericata* are capable of laying nearly 2,000 eggs. Three isolated females whose oviposition was followed completely laid 1,048, 1,471, and 1,883+ eggs respectively and five placed together

in one cage laid 8,090+ eggs. The average for these eight females was, therefore, 1,561·5. It is improbable, however, that so many eggs are usually laid in nature, because as it becomes older the fly is less agile and is therefore less likely to find carcases for oviposition and more likely to fall a prey to its enemies.

The first batches of eggs laid are almost completely viable, and the slight loss I sometimes noted in my rearings may well have been due to faulty technique (especially to slight and unnoticed injury in breaking apart the groups of eggs) or to the very close inbreeding to which my stock was subjected for other purposes. Of the 2,825 eggs considered in Tables I and II (below, and p. 239), 2,714, or 96·1 per cent., hatched in spite of the considerable manipulation their separation and counting had entailed. Eggs laid late in the life of the females showed a greater loss, but as the eggs seemed themselves to be of normal size this again may have been due to my method, for the males, which are much shorter-lived than the females, were not replaced when they died. Isolated females without males sometimes produced belated eggs which did not hatch; and often when a single pair of flies were put together the female laid infertile eggs—presumably mating had not occurred.

When ample food is available there is very little loss during the feeding period of the larval life (see columns 2 and 3 in Table I, below) and unless the larvae are very much undernourished they usually proceed to pupation (compare columns 3 and 5 in Table II, p. 239). Again, under favourable conditions, most of the individuals that pupate succeed in emerging as adult insects. In short, in many rearings I have obtained a complete emergence, an adult from every egg.

Allowing generously for all these losses it may safely be claimed that with an ample supply of meat and suitable environmental conditions at least one thousand progeny can be reared from a pair of *Lucilia sericata*, and for purposes of argument this may be taken as the potential reproductive rate of the sheep blowfly.

Overblowing.

In the development of my rearing technique one of the first problems was to determine the amount of food it was necessary to supply the larvae of *Lucilia sericata* for their proper development. In a preliminary experiment six lots of minced beef, weighing 10·00 gm. and entirely comparable, were provided with 30, 35, 40, 45, 50, and 55 eggs respectively, the eggs all having been laid within fifteen minutes. The result is shown in Table I.

TABLE I.

Showing the number and average weight of the larvae obtained when different numbers of eggs from 30 to 55 were placed on similar portions of lean minced beef each weighing 10·00 gm.

Experiment	No. of eggs placed on meat	No. of eggs that hatched	No. of full-grown larvae obtained	Average weight of larvae in gm.
15—A	30	29	29	0·047
B	35	34	32	0·050
C	40	39	38	0·048
D	45	45	42	0·044
E	50	45	39	0·047
F	55	54	54	0·050

This preliminary experiment served to show that the average weight of a fully grown and amply nourished larva of *Lucilia sericata* is about 0·050 gm. and that at

least 54 individuals of that size can be reared on 10·00 gm. of minced lean beef, but it did not even foreshadow a limit to the number of larvae that can be so reared. Moreover, in the course of this experiment it was realized that a very important factor in the natural control of *Lucilia sericata* was bound up with the matter of the larval food supply, and the experiments were continued with a view to ascertaining the behaviour of the flies when the supply was short.

Table II sums up the results of four experiments on this subject. Each group of figures represents a single experiment and is strictly comparable within itself. The four experiments also were designed to be as comparable as possible, but slight differences in treatment, environmental conditions, and the food provided could not be avoided. In each case the number of eggs indicated was placed on 10·00 gm. of minced lean beef. As the number of eggs in the experiment increased, so did the time required for their laying, and in the two experiments 16 and 17 the eggs were laid over periods of 4 and 2½ hours respectively.

TABLE II.

Showing the number and average weight of the larvæ obtained when different numbers of eggs from 40 to 300 were placed on similar portions of lean minced beef each weighing 10·00 gm.

Experiment	No. of eggs placed on meat	No. of eggs that hatched	No. of living individuals obtained on 8th day	Average weight of same in gm.	No. of puparia formed	Loss in larval stage
16—A ...	40	37	36	0·050	36	1
B ...	50	47	47	0·049	47	0
C ...	60	51	50	0·051	50	1
D ...	80	74	67	0·050	67	7
E ...	100	96	87	0·047	87	9
F ...	120	106	95	0·043	95	11
G ...	140	127	111	0·039	111	16
17—A ...	140	135	133	0·029	131	4
B ...	160	152	145	0·027	143	9
C ...	180	176	170	0·025	164	12
D ...	200	189	184	0·023	177	12
E ...	220	214	207	0·021	192	22
F ...	240	234	230	0·018	192	42
46—A ...	260	258	223	0·017	125	133
B ...	280	272	212	0·0165	128	144
47 ...	300	300	256	0·0165	137	163

The following points in Table II should be especially noticed :—

(1) Taking the average weight of a fully grown and amply nourished larva of *Lucilia sericata* as 0·050 gm., 67 normal individuals were reared on 10·00 gm. of minced lean beef.

(2) When more than 67 individuals fed on 10·00 gm. of meat the weight of the individuals decreased. The average weight of individuals living on the eighth day reached a low point in my experiments of 0·0165 gm., but only the larger individuals among these proceeded to pupation.

(3) As increasing numbers of larvae fed on the portion of meat the number of individuals lost in the larval stage increased.

(4) The increase of the loss in the larval stage was disproportionate to the increase in the number of eggs placed on the meat, so that finally, from the later portions, fewer puparia were obtained than the meat was actually

capable of producing. This result may be attributed to the use of food by many first- and second-stage larvae that were not able to complete their development, but depleted, by feeding, the amount of food available to those that would have been able to mature. The significance of this result in the natural control of blowflies will be discussed in the next section.

(5) The number of puparia produced on 10 gm. of meat reached a maximum of 192 and then fell. Besides the figures given in Table II there is another indication that this number is near the limit. Although fewer larvae competed in 17E than in 17F the same number (192) pupated in each, but from this same number of puparia 181 adult flies emerged in 17E and only 174 in 17F. Presumably several very small individuals in 17F were able to attain pupation but not strong enough to complete their development.

The Natural Control of Lucilia sericata.

The results of my experiments on overblowing, described above, suggested an investigation of this principle in nature, and pieces of beef and whole small mammals were exposed to natural blowfly attack. In one case, 156 gm. of meat exposed in bright sunshine bore 5,645 eggs, principally of *Lucilia sericata*, after only five hours, although this amount of meat could support no more than 1,050 full-sized and certainly not more than 1,560 normal though somewhat under-sized individuals. It was immediately apparent, without counting, that the whole carcases were grossly overblown within a few hours. After a day or two, thousands of partly grown larvae began to migrate from them. From such carcases, on which thousands of eggs had been deposited, comparatively few adults of *Lucilia sericata* were obtained.

My own small-scale experiments in this matter are not worth detailed record since Holdaway (1930) has published some notes on his very excellent large-scale studies of the subject. Holdaway's experiments show the enormous reduction from a population of 48,562 *L. sericata* twenty-four hours after exposure to a final emergence of only 231 flies ; and again from 63,200 Lucilias (of two species) to only 30.

Holdaway points out that " the greatest factor in the reduction of the fly population within the carrion is Dipterous competition and its associated predatorism," but although I had sent him a copy of my earlier note on over-blowing (Salt, 1930) he apparently failed to notice the very striking agreement of my laboratory and his field results. While *Calliphora*, *Sarcophaga*, *Chrysomyia*, HISTERIDAE, and other members of the carrion fauna undoubtedly play a part in the reduction of the numbers of *Lucilia*, either by simply competing for the food or by predatism, it is clear from my laboratory experiments that a very great reduction takes place owing to the competition of the Lucilias among themselves and in the entire absence of other forms. While admitting the importance of the rôle of these other forms, I must insist that they merely aggravate a condition that would still obtain without them—the population of *Lucilia sericata* is enormously reduced simply by its habit of laying more eggs on a carcase than the tissues can support.

It seems clear from these experiments that *Lucilia sericata* is one species that normally, in England and France, completely saturates its environment—the factor that chiefly limits the increase of its population is the shortage of carcases. It is interesting to note, however, that the potential reproductive rate of *Lucilia* is so high that even if more carcases became consistently available they would soon be overblown and the same competition and self-elimination would occur.

One of the effects of overblowing in my laboratory experiments was the reduced size of the flies obtained. Mr. F. Wilson has asked me how it is, then, if carcases in the field are usually overblown, that wild specimens of *Lucilia sericata* are not very small. Small specimens are indeed sometimes taken in the field, though I have never seen wild specimens so small as some of my starved individuals. Moreover, ample

feeding in the laboratory produces individuals only slightly if at all larger than the average specimens collected outside. The question, then, is pertinent. I have no experimental evidence that will form an answer but offer a suggestion that helps, at least, to explain the matter.

In my experiments the eggs placed on a quantity of food were all of the same age, so that the resulting larvae were of about the same size and strength and competition was close. Normally, in the field, some eggs are laid before others. The larvae from the early eggs are greatly favoured in the competition for food in being less likely to be pushed off the meat by larvae of their own species, in being more able to withstand the competition of larger species of carrion-feeding Diptera, in being able more readily to penetrate the tougher tissues of the carcase, and in being more likely to avoid or repel the attack of a predator. In brief, I suggest that the survivors are larvae from the first eggs laid on the meat and that these, owing to their several advantages, are able to nourish themselves completely and produce full-sized flies.

Unfortunately, I was unable to study the effect of partial starvation during the larval period on the reproductive capacity of the resulting female flies.

Rearing Alysia manducator, Panzer.

The work of rearing *Alysia manducator* at the Farnham House Laboratory was initiated in 1927 by Dr. J. G. Myers, who published his observations in two papers (Myers, 1927, 1929). Myers' method consisted in the liberation of collected specimens of *Lucilia sericata* and *Alysia manducator* in a large insectary where freshly killed cats were exposed on enamel trays. The fully-fed maggots moved off the carcases and came to rest between sheets of brown paper from which they were gathered and placed in sand in large jars. This method provided an enormous supply of maggots, but the percentage of parasitism was rather low. Moreover, no very precise data could be obtained from it.

After much trial and experiment I found a purely artificial method of parasitization to be the best. About fifty nearly full-grown larvae of *Lucilia sericata* were removed from the feeding medium and placed in a porcelain dish containing a little fresh minced meat. Five or six mated females of *Alysia manducator* were introduced and usually began at once to parasitize the maggots. Females that failed to do so or that became exhausted were replaced, so that five or six parasites were always actively engaged. The parasitized maggots were removed, as soon as the parasites moved off them, to an ordinary rearing jar (fig. 1) where they could proceed to pupation. From time to time fresh maggots were added so that the number available to the parasites remained about fifty. By this method a laboratory assistant could easily obtain twelve to fifteen hundred parasitized larvae in a day or, allowing for deaths and for cases (see below) of paralysis without parasitization, about one thousand *Alysia manducator*.

The Reproductive Rate of Alysia manducator.

Altson (1920, p. 209) counted the eggs in the ovaries of twelve females of *A. manducator* and found that they ranged from 325 to 416 with an average of 366. He found, however (p. 215), that in practice " it took a total of 39 females to reproduce definitely 1,306 individuals exclusive of over-parasitized larvae—an average of 33·74 each, or only 9·89 per cent. of their average egg-capacity." Graham-Smith (1919, p. 380) showed that the ovaries of one female contained at least 549 eggs, of which at least 206 were deposited in maggots and 193 developed to adult parasites. Another female, unfertilized, deposited at least 83 eggs, of which 71 developed into male adults.

The highest actual reproductive rate I have observed was 101. A mated female *Alysia* five days old was placed in a large petri dish with a small quantity of fresh

minced meat and a number of larvae. As the maggots were paralysed they were removed. After an hour and a half the parasite seemed to be tiring and the poison of the sting was obviously less effective. Many larvae were partly stung and then escaped. After two hours the *Alysia* was removed to a clean vial and fed on a split raisin, 99 larvae having been stung to immobility. The following day, in two hours in the morning, the same parasite again paralysed 99 larvae and was again removed and fed. In two hours the same afternoon it stung 93 larvae. It was placed with food overnight and the next morning was still alive although feeble. On being presented with maggots it attempted to sting one or two passing near it but was unable and was removed. In the afternoon it was dead. On dissection only 11 eggs could be found in its ovaries. During each of the three periods of parasitization the temperature varied only between 20° and 21·5°C.

The paralysed maggots behaved as follows :—

	Stung	Pupated	Produced flies	Produced *Alysia*
1st period ...	99	84	10	74 (18♂ 51 ♀ 5 ?)
2nd period ...	99	97	79	18 (9♂ 8 ♀ 1 ?)
3rd period ...	93	84	75	9 (3♂ 4 ♀ 2 ?)

It is interesting to notice that the rate of oviposition under these conditions was very constant—99 in each of the first two periods with only the comparatively slight falling off to 93 in the third period when the parasite was tiring. Also it should be observed that the proportion of paralysed maggots that were actually parasitized was greatest in the first and least in the third period.

Several other females treated in the same way laid fewer eggs, and when parasites were placed on a carcase with a number of maggots I found, as Altson had done, that they succeeded in laying only a small part of their supply of eggs before they became completely exhausted by their struggles with the larvae and by their efforts to free themselves from the adhesion of the filth in which they laboured.

The few accurate figures available do not justify the taking of an arithmetical average and I content myself with expressing my opinion that a single female of *Alysia manducator* under the most favourable conditions seldom lays more than 200 eggs and that the average effective rate of reproduction in nature is less than 50.

The Value of Alysia manducator as a Parasite of Sheep Blowflies.

The value of a parasite as a controlling agent is largely dependent upon its reproductive rate relative to that of its host. The potential rate of reproduction of *Lucilia sericata* may be considered, as shown above, to be in the neighbourhood of one thousand, but its effective rate of reproduction, owing to the elimination of an enormous number of larvae by competition, is very much less. Consequently, two very different estimates of the value of *Alysia manducator* as a parasite are obtained according as one considers its immediate effect on the numbers of its host, based on observed percentages of parasitism, or on its ultimate effect as a controlling agent, based on its potential reproductive rate relative to that of the blowfly.

Collections of puparia made in the field are sometimes very heavily parasitized by *Alysia*. Of 16,028 puparia collected by Graham-Smith (1919, p. 379) in the autumns of three years, 7,041, or 43 per cent., were infested with *Alysia manducator*, and of 4,787 puparia collected during the summer months of two years, 508, or 10 per cent., were infested. In two lots of material collected on 27th July, Altson

(1920, p. 215) found the percentage of parasitism by *Alysia* to be 23·12 and 52·32 per cent. respectively. Myers (1927, p. 220) mentions rates of parasitism in different lots of puparia ranging from 0 to 80 and nearly 100 per cent. From four carcases exposed in both sunny and shady situations in September and October, 1929, I obtained 2,897 puparia of which at least 2,047, or 70·7 per cent., were parasitized by *Alysia*.

These observed rates of parasitism, however, require a correction, for they exaggerate the importance of *Alysia*. Altson (1920, p. 211), Holdaway & Evans (1930), and Davies (1930) have recorded that parasitization by *Alysia manducator* stimulates maggots of *Lucilia sericata* to pupate. In corroboration it may be mentioned that during the autumns of 1928 and 1929 some thousands of parasitized individuals were selected at the Farnham House Laboratory by this means—the unparasitized maggots entered the usual winter diapause, while the parasitized larvae pupated and were sent abroad. This, of course, is only a specific case of a well-known phenomenon (*cf.* Pantel, 1912, pp. 121-124). However, there is a further interesting fact about this hastening of pupation in *Lucilia sericata*, namely that starved, half-grown larvae that would normally fail to pupate may yet, under the stimulus of the parasitization, accomplish pupation and serve as a satisfactory host of *Alysia*. Apparently *Alysia* can develop on less nourishment than is required by *Lucilia*—certainly *Alysia* adults may be much smaller than the smallest *Lucilia*—and a carcase capable of yielding only a certain number of adult *Lucilia* may yield a greater number of *Alysia* and *Lucilia* adults taken together. Percentages of parasitism of *Alysia* based on collections of puparia, then, exaggerate the actual controlling influence of the parasite, since many *Alysia* adults emerge from tiny puparia that, in the absence of the parasite, would never have been formed.

TABLE III.

Showing the effect of a consistent parasitism of (1) 90 *per cent.* (2) 99 *per cent. by* Alysia manducator *when the available food limits the number of maggots to* 1,000.

	Eggs laid	Surviving maggots	♂ *Alysia* and *Lucilia*	♀ *Alysia*	♀ *Lucilia*
(1)	—	1,000	500	450	50
	50,000	1,000	500	450	50
	50,000	1,000	and so on		
(2)	—	1,000	500	495	5
	5,000	1,000	500	495	5
	5,000	1,000	and so on		

These rates of parasitism considered alone are rather impressive. From its frequence of 50 to 70 per cent. in some collections of puparia it is clear that *Alysia* does, especially in the autumn, considerably reduce the numbers of adult flies one actually finds about. Since the economic damage, the striking of sheep, depends on the adult flies, there would seem to be a distinct advantage in having fewer flies present.

When, on the other hand, one considers the great discrepancy in the reproductive rates of *Alysia* and *Lucilia*, one must admit that this parasitism can have little *ultimate* effect on the blowfly population. Not only is the potential reproductive rate of an individual *Lucilia* at least ten times that of a single *Alysia*, but also the life-cycle of the fly is shorter, so that it may have four generations in one season while the parasite has only two.

Even neglecting the last point and assuming that the generations of *Alysia* and *Lucilia* were synchronized, the blowfly could consistently lose more than 99 per cent. of its population in each generation to *Alysia* and yet maintain its numbers. For example, let us assume that in a given area there are sufficient carcases to support 1,000 maggots in each generation and, disregarding other controlling agents for the moment, consider (Table III) the case of a consistent parasitism by *Alysia* in each generation of (1) 90 per cent., (2) 99 per cent.

Obviously the number of adult flies is less when the parasite destroys 99 per cent., but it is equally clear that against a parasitism of 99 per cent. as against one of 90 per cent. the blowfly maintains its population so as to use fully all the available carcases.

Now it is inconceivable that *Alysia* could ever consistently parasitize 99 per cent. of the *Lucilia* larvae no matter how large its own population, because in a carcase a certain number of maggots are usually inaccessible to the parasite and may enter the ground to pupate under the remains without ever having been exposed to attack. The reproductive ability of *Lucilia* is such that the escape of only a very few individuals in each generation ensures the maintenance of a large population. In brief, *Alysia manducator* cannot reduce the population of *Lucilia sericata* below the point at which the blowfly fully exploits all the available carcases.

The conclusion of this discussion is plain. Although *Alysia manducator* reduces to some extent the number of adult flies one finds about, it has no value as an *ultimate* controlling agent of *Lucilia sericata*.

Suggestions on the Blowfly Problem.

Having had no opportunity of studying the blowfly problem in a sheep-rearing district—in other words, where it *is* a problem—I hesitate to discuss practical measures. On the other hand, having spent so much time investigating certain fundamentals of the question, albeit in the laboratory, I feel an obligation to relate my findings with practice. I therefore make the following remarks, claiming nothing more for them than the rank of suggestions.

Applying the conclusion of the preceding section to the practical problem of blowfly control, the question first arises whether, where *Alysia* fails, another parasite might succeed. I think not. Of all the known parasites of blowflies *Alysia manducator* is best, because it acts at the optimum time. It parasitizes the larvae, namely, when they are almost full-grown, after the environmental factors and overblowing have taken their enormous toll. Its parasitism, therefore, is actually effective. Parasites such as *Figites anthomyiarum* and *Kleidotoma marshalli* (James, 1928) that attack the larvae in their early stages are far less effective, because a very large proportion of the larvae they destroy would die in any case. *Mormoniella brevicornis* and other parasites of the pupa are effective but fail in control because only a small proportion of the puparia, namely those exposed on the surface of the ground, is accessible to them.

As for predators of blowfly larvae, Myers (1929, p. 357) sometimes obtained " practically pure cultures " of the Anthomyiid, *Hydrotaea dentipes*, whose maggots are predatory. Holdaway (1930, p. 648) considers some of the carrion beetles more or less definitely associated with Diptera, such as the HISTERIDAE, of some significance. While many of these predators may be beneficial, on the evidence discussed in previous sections I am of the opinion that none is or could be ultimately effective in controlling sheep blowflies.

Since, in my view, the numbers of *Lucilia sericata* are very largely controlled by the competition of the larvae for a dearth of food, anything that increases that competition is beneficial. Therefore, *Sarcophaga*, *Calliphora*, *Chrysomyia*, and other Dipterous competitors must be considered of importance. There is a crying need

for reliable information concerning the original colonizer on living sheep—the species responsible for striking. If it could be shown that the one species, *Lucilia sericata*, alone was responsible, it might even be useful, for a time at least, to protect other, competing species.

In spite of these minor possibilities, I am of the opinion that the reproductive rate of *Lucilia sericata* is such as to preclude the method of biological control.

If the conclusion is correct, and it can hardly be otherwise, that the shortage of carcases chiefly limits the blowfly population, a direct method of control—the careful destruction of all carrion, together, perhaps, with the use of trap carcases—would seem to be of first importance.

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A COMPARISON OF THE LARVAE OF *EUMERUS STRIGATUS*, FLN., AND *EUMERUS TUBERCULATUS*, ROND. (SYRPHIDAE).

By W. E. H. Hodson, A.R.C.S.,

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Some years ago the writer[2] published an account of the bionomics of the two species of *Eumerus* whose larvae attack narcissus and other plants. In this account it was pointed out that *E. tuberculatus*, first recognised as occurring in Britain by Collin[1] in 1920, was far more abundant than *E. strigatus*, which had been described by Verrall[4] in 1901. This finding was entirely contrary to expectation and threw serious doubt upon the accuracy of many previous records of injury to plants in which *strigatus* was invariably cited as the culprit. At the same time it explained in a large measure the absence of reports of *Eumerus* attacking onions in Britain, for in those countries in which damage to onions is of common occurrence the predominant species appears to be *strigatus*. In view of the foregoing, and of the fact that the successful cultivation of onions is exceedingly difficult and at times impossible in regions where attacks by *Eumerus* are experienced, it is desirable that further information be obtained as to the occurrence of *strigatus* in Britain.

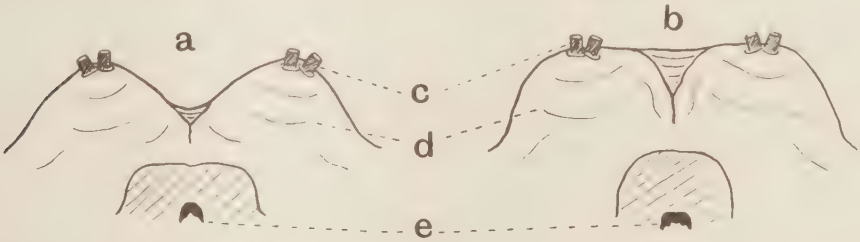


Fig. 1. Semi-diagramatic representation of buccal region of (*a*) *Eumerus tuberculatus*, Rond.; (*b*) *Eumerus strigatus*, Fln.; (*c*) antennae; (*d*) antennal tubercles; (*e*) tip of mandibular sclerites.

The writer[2] has shown that both species under consideration attack narcissus, that both may be bred from a single bulb, and that their life-histories in this host are identical. In this publication no serious attempt was made to separate the larvae with accuracy.

Collin[1] was principally concerned with the separation of the species in the adult form. At the same time some attempt was made to separate the larvae, but Collin was handicapped by lack of data and shortage of material and was thus unable to define specific differences.

The writer has for a number of years collected batches of larvae, preserved portions of each batch, and bred out the remainder. In some cases flies of both species have emerged from individual batches. More frequently all emergences have been *tuberculatus*. In two cases only, from iris and parsnip respectively, have *strigatus* alone emerged. In addition to these larvae, numbering some 200, further *strigatus* material has been obtained from Omsk in Russia and from the Swedish island of Gotland.

As is to be expected, the larvae of two such closely related species show striking similarity. It has nevertheless been found possible to detect small differences which almost invariably enable an accurate determination of the species to be made,

although occasionally an individual larva is found which cannot be placed with certainty. Provided, however, that three or four specimens are available for study, no difficulty should be experienced.

Reference should first be made to a recent publication[3] in which the larva of *E. tuberculatus* is described in detail and figured.

In the following key special attention should be paid to the mandibular sclerites and to the tubercles bearing the antennae, as these provide the most useful clues as to the species.

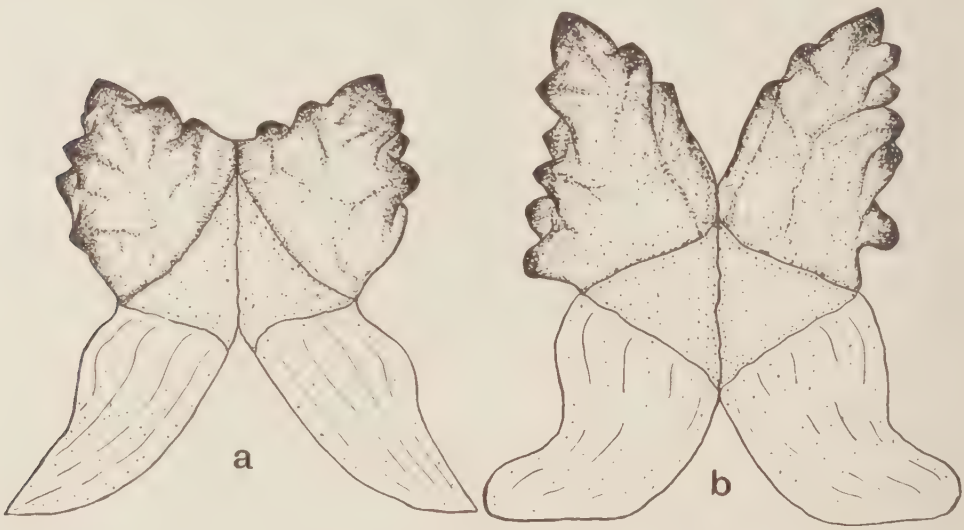


Fig. 2. Camera lucida drawing of mandibular sclerites greatly enlarged of (*a*) *E. tuberculatus*; (*b*) *E. strigatus*.

Key to Larvae.

	E. strigatus	*E. tuberculatus*
Anterior spiracular processes	colour darker	colour lighter
Fused posterior spiracular processes	shorter, wider, colour darker	longer, more narrow, colour lighter
Antennae	groove between tubercles bearing the antennae shallow or absent	groove pronounced
Minute scattered spines	colour darker, less abundant	colour lighter, more abundant
Larger spines	colour darker, shorter	colour lighter, longer
Anal tubercles	appreciably darker than remainder of integument	unicolorous with or only slightly darker than remainder of integument
Mandibular sclerites	larger, teeth more numerous, usually 7 prominent pairs, rarely less than 6	smaller, teeth less numerous, usually 5 prominent pairs, very occasionally 6

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A STUDY OF THE LIFE-HISTORY AND CONTROL OF *CERAMBYX DUX*, FALD., A PEST OF CERTAIN STONE-FRUIT TREES IN PALESTINE.

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(Plates XI & XII.)

A long-horned beetle, *Cerambyx dux*, Fald., is a very serious pest of apricots, peaches, and grafted and wild almonds in Palestine. Its ravages are most probably not confined to these trees and further investigations will undoubtedly enlarge the already important list of food-plants. In localities around Jerusalem such as Beit-Jala, Artas, Bethlehem, El Maliha, and Ein Karim (approximate altitude 2,600 feet above sea-level), this pest has been allowed to establish itself over a long period of time and to such an extent that, if immediate and rigid control measures are not undertaken by the growers, apricot and peach trees will, sooner or later, disappear from these localities. These fruit trees can be cultivated without irrigation, which is of great advantage in Palestine, where water is scarce ; the fruit fetches good prices both in the local markets and also in Egypt. Their cultivation is therefore of vital importance, especially to the population of the hill country, where conditions of life are difficult and every kind of loss is accentuated. In Jersualem, where almonds, apricots and peaches are planted in household-gardens, not a single healthy tree can be found, and many of them have already succumbed to the attacks of this beetle. In the coastal plain the writer has found this insect in almond trees at Haifa and in apricot and almond trees in villages north of Acre. No records are available of its presence in the coastal plain south of Haifa or in the Jordan Valley.

Description of Early Stages.

The egg is oval and markedly pointed at one end ; it measures 4 mm. in length and 2 mm. in width. The colour is dirty white and the whole surface is roughened like that of a rasp.

The larva is fleshy, of a dull white colour with a distinct yellowish tinge, and its length, when full-grown, is from 55 to 65 mm. The small, brown head is invaginated into the prothorax and contains two strongly developed and powerful mandibles. The broadest of the segments is the prothorax, measuring from 15-19 mm. in width ; from here the body tapers gradually to the anal segment, which is the narrowest, measuring from 8–12 mm. The three thoracic segments bear three pairs of rudimentary, brownish legs. The pronotum and the pleurites of the prothorax are partly chitinized and of a brownish colour. The prothorax rises at an angle of forty-five degrees from the head and is used, with the head, to push the frass out of the tunnellings. Pseudopods on the dorsal and ventral sides facilitate movements within the borings. The newly hatched larva, except in size, entirely resembles the full-grown one. Its length is 5 mm., the width of the middle of the body 1·25 mm., and the prothorax is 2 mm. in breadth.

The pupa is at first of a dirty white colour, darkening later. It is 45–55 mm. long and rests in a cell prepared by the larva.

Life-history and Habits.

Under field conditions this insect completes its life-cycle within two years. Emergence from the pupal stage begins about 15th May and continues till about 15th June; at the end of August these adults die after mating and egg-laying. The adult beetles are very sluggish in their movements and in the morning become active only on a rise of temperature. During flight the body is kept in an upright position and the long antennae oscillate. The adult beetles when settled on a tree and suddenly disturbed will at once drop to the ground; on being molested in any way they stridulate.

Mating takes place a few days after hatching and is performed several times. Copulation lasts from 40 to 70 seconds and during this time the male performs stroking movements with its palpi on the elytra of the female near their base. In breeding cages kept in an open air insectary the sexual life was polygamous. A female deposits 30–40 eggs, which are laid singly in cracks and crevices of tree-trunks and main branches, on wounds and especially on frass under dead bark. The female is very careful in the selection of a place for her eggs and crawls along the tree with exserted abdomen, placing it in every crack and crevice in order to select the most suitable sites. A very favourite place for egg-laying is the crotch of the tree, which is a well-shaded and protected spot. In breeding cages all eggs were deposited on that side of a branch which was not exposed to the light, and sometimes eggs were found under watch-glasses in which syrup had been placed for the beetles. The eggs are gummed by means of a sticky material to the surface of the bark (Pl. xi, fig. 1).

Trees under the age of eight years, unless wounded, are very seldom attacked by this pest because, having smooth bark, they do not provide the required protection for the eggs. Eggs which were exposed experimentally to the direct influence of the rays of the sun failed to hatch. Eggs hatch within a period of one to three weeks depending upon temperature. As soon as the head of the larva appears out of the eggshell it starts to bore at once into the tree, filling the eggshell with fine sawdust-like excrement. The young larva feeds first on the bast and cambium and with advancing age bores into the wood itself, making irregular tunnels and throwing out, through holes made in the trunk, large quantities of frass, which is at times mixed with gum from the tree. In heavily infested trees heaps of frass are found around the base of the trunk; large quantities also remain in the tunnellings and under the bark, where patches of bast, cambium and wood have been destroyed and turned into sawdust. The larvae are mainly stem-borers (Pls. xi, fig. 2; xii, fig. 4); they seldom, if ever, penetrate to the roots. The most frequently destroyed part of the tree is found at the crotch and downward therefrom to a distance of about 60 cm. from the ground. This may be explained by the fact that most of the eggs are deposited in the crotch. In heavily infested trees this part of the stem is riddled with larval borings, and it frequently happens that strong winds break down main branches and expose the destructive work of the larvae. Thirty to fifty larvae of different sizes and ages may be found in a heavily infested tree. Their boring activities are sometimes distinctly audible on laying the ear on the trunk.

It is obvious that the fruit-bearing powers of such heavily infested trees are greatly reduced. In addition, a Scolytid beetle, *Scolytus amygdali*, Guér., takes advantage of the weak condition of such trees and attacks them secondarily, causing the death of the main branches and at times killing the whole tree.

The larval stage lasts 15–16 months. The larvae show very little activity during the colder winter months (*i.e.* from the middle of December till the end of February). Prior to pupation the larva prepares a cell within its tunnel by clogging the ends with frass. This cell is then sealed up from within and at both ends with a cement-like material, and finally pupation takes place. The pupal cells (Pl. xii, fig. 2) are mostly prepared in tunnels running parallel to the axis of the trunk or at an

angle of 45 degrees thereto. The quantity of sap within the trees has a great influence upon the development of the larvae and beetles. Larvae which are one year old and which happen to be in a tree when it dies can complete their life-cycle, but the beetles of such larvae are smaller than those whose larvae develop under normal conditions. In the laboratory some newly-hatched larvae were placed between sheets of blotting paper which had been soaked with various syrups. For a few days syrup was added, but after that the blotting paper was allowed to dry and become like parchment. One larva lived for a whole year under such conditions; its size at the completion of this period was, however, only twice that of a newly-hatched larva.

The complete life-cycle of this beetle runs as follows in the hill districts near Jerusalem:—Egg-stage, 1–3 weeks (during May or June); larval stage, 15–16 months (from June of one year till August–September of the following); pupal stage, 1–2 months (during August–November); dormant adult stage within the pupal cell, 7 months (from November till May).

Methods of Control.

Control measures are directed against the beetles and larvae and consist in:—(1) Removal of dead bark from the trunk and main branches and all frass from the areas exposed by such bark removal; (2) plugging of all holes in the trunk and main branches with cement; (3) treating all new borings which appear after cementing of trees with carbon bisulphide; (4) felling and removal of heavily infested and dead trees; (5) whitewashing of trunks and main branches.

Removal of dead bark and frass.

It is highly important to remove all remnants of the destructive larval work. Such places are especially frequented by egg-laying females and also provide shelter for other undesirable insets. Four tools serve this purpose well; a sharp adze, a screw driver 25 cm. long and 8 mm. broad at the point, a carpenter's flat chisel, and a sharp garden knife. Care must be taken to make no wounds in the healthy bark during this operation. The frass must also be removed, by means of the chisel, from tunnellings which cannot be entirely opened. A sharp-pointed, flexible wire introduced into such tunnellings will kill any larvae or pupae in them.

Clogging holes with cement.

After the trees have thus been cleaned all holes in the trunk and main branches must be cemented. This serves a double purpose: firstly, it prevents the emergence of adult beetles and consequent egg-laying; and secondly, it compels the enclosed larvae to bore new holes in order to push out their frass. The larvae thus indicate exactly their whereabouts. This is important when treating neglected trees which contain a great number of holes. Cementing of holes also prevents the entrance of fungi and other insects. The best results are obtained from a good quality cement mixed with equal parts of sand. In heavily infested trees, where large parts of the wood have been destroyed and must be replaced by cement, it is advisable to drive in nails and, by joining them with flexible wire, create a net, which will help to keep the cement in position. Space must be left so as to ensure an easy and smooth growth of bark over the cemented areas. After cementing has been completed all frass and pieces of dead bark must be removed from around the tree and buried deeply in the ground or burnt. Cementing of trees should be completed by the end of April in order to prevent the emergence of beetles.

Treating holes with Carbon Bisulphide.

As mentioned before, after cementing all holes, any larvae that may have been overlooked will bore new galleries in order to push out their frass. All newly-bored

holes are treated with 1–2 cc. of carbon bisulphide. This quantity is sufficient to kill a larva in its tunnel. The fluid may be injected by means of a hypodermic syringe, but the constant charging of this is troublesome and causes a loss of time. The writer successfully overcame this inconvenience by converting an oilcan into an injector by affixing the needle of a hypodermic syringe to the end of the delivery tube in the place of the usual cap. The required quantity of bisulphide to be discharged can then be regulated by the strength of pressure exerted on the slightly convex walls of the can.

Before injecting the fluid, the frass is first removed from the entrance of the hole and, where necessary, a pointed wire is pushed into the hole in order to facilitate introduction of the injector. After the injection of carbon bisulphide the holes are best closed with grafting wax, and all treated trees must be inspected periodically and all freshly made holes injected. It must not be forgotten to clean away the frass from the ground under the tree after each treatment. Owing to the high inflammability of the carbon bisulphide, precautions are necessary. For field transport one gallon drums are most suitable ; from these drums the carbon bisulphide is transferred to 500 cc. tin containers, which should be efficiently closed by means of a screw-stopper.

Removal of heavily infested and dead trees.

All heavily infested trees in the orchard that have been riddled by boring larvae and bear but little fruit should be felled as well as all dead ones. Felled trees must be removed immediately from the orchard, cut into logs and then chopped into small pieces in order to prevent the insect from completing its life-cycle. On visiting infested orchards the writer has on many occasions found piles of dead trees which have been killed by this pest heaped up around the houses of orchardists ; thus the growers themselves have facilitated the spread of the pest. In other countries where fuel of all kinds is cheap the immediate burning of such infested trees would be indicated, but such advice would not be in favour with the rural population of Palestine, among whom fuel is scarce and expensive, and every little bit of wood found on the road is picked up carefully and stored. In town gardens, where fruit trees are planted more for ornamental purposes, even if they are heavily infested, they can be treated as indicated with excellent results. Trees which have been infested secondarily by Scolytid beetles must be barked after felling and all removed bark immediately burnt.

Whitewashing of trunks and main branches.

After cementing and treating the trees with carbon bisulphide, the trunk and main branches should be well whitewashed. The whitewash seems to have a deterrent effect upon the egg-laying female. In the breeding cage no eggs were deposited on pieces of almond branches which were whitewashed and placed among other pieces.

Technical Methods utilized in Breeding Cerambyx.

Heavily infested almond trees were felled, cut into logs 32cm. long, numbered and placed in 4 gallon petrol tins similar to those used by Buxton[2] and advised by Beeson.[1] Each tin was tightly closed by means of a cone-shaped lid, ventilated on the top. A test-tube was attached by means of india-rubber tubing to a short cylindrical piece of tin, soldered to the side of the tin a bit above the bottom ; emerging beetles were thus trapped, removed daily and placed in a breeding cage specially designed by the writer.

This cage consisted of two wooden, detachable parts. The lower part is a solid box 26·5 cm. high, 47 cm. broad, and 72·5 cm. long. The upper part is 54 cm. high,

the other two measurements corresponding to those of the lower part. This upper part was fitted with a hinged lid fastened down with hooks. The front and hind walls, as well as the lid of this upper part, consisted of frames fitted with very fine-meshed brass netting; in each of the wooden side walls was a small close-fitting door, 10 × 10 cm. In the centre of each of these doors was drilled a hole 15 cm. in diameter to which was attached a fitted zinc tube that projected outwards, so that a test-tube might be attached to it by means of rubber tubing. The interior of the cage was painted dull black.

To facilitate the handling of beetles enclosed in the cage for breeding or observational purposes the well-known attraction of insects to light was utilized. To this end special fittings were made so that the sides furnished with netting could be rendered light-tight by means of wooden boards which fitted closely into the wooden framing of the wire. As soon as the cage had been made light-tight the enclosed beetles made their way to the circular holes to which test tubes had been fitted as described above. The lower part of the cage was filled with soil. Healthy branches from infested almond trees were cut into logs and placed in the cage. The beetles were fed on syrup. Water was also given and the soil in the box kept moist. All eggs deposited were removed daily and placed on watchglasses, which were kept on damp soil in boxes and covered with very fine-meshed brass wire cages. Larvae which hatched were removed daily.

In order to reproduce as closely as possible the natural conditions under which this pest exists in its larval stage the following method was adopted, which gave full facilities for observation. Branches of almond trees 2·5–3 cm. in diameter were cut into pieces each 15 cm. in length. A piece of combustion glass tubing, 10 cm. in length, was placed on one end of these pieces and the other end of the tube was filled with moistened frass to a height of 3 cm. and pressed down slightly. The frass was obtained from infested trees and carefully examined for the possible presence of eggs of *Cerambyx*. Four to five holes were made by means of a needle in the frass and one freshly hatched larva placed in each hole. This was then covered with another layer of frass half a centimetre thick. The frass was kept moist by adding a few drops of water from time to time. These pieces of wood with glass tubing attached were then stood in receptacles containing water, the end of the wood being immersed in water to a depth of some 3 or 4 cm. As soon as the tunnel of a boring larva reached the water-level in the bottle the piece of wood was removed and substituted by another one of greater diameter (Pl. xii, fig. 1). Over this new piece of wood a piece of glass-tubing was placed into which the old piece with the boring larva was also introduced. A layer of about 2–3 cm. of moist frass was placed between the two pieces of wood, and in the majority of cases the larva continued, undisturbed, to bore from the old piece to the new one. Larvae obtained after a year from these breeding experiments were only slightly smaller than those of a similar age breeding under natural conditions. To observe the effect of the carbon bisulphide on the larva, a glass tube one metre long and 17 cm. in diameter was tightly filled with somewhat moist frass and tightly stoppered at both ends. A nearly full-grown larva was then placed at the bottom and allowed to tunnel half-way up the tube. One cc. of carbon bisulphide was then injected. The larva reacted by attempting to close up the passage whence came the fumes of the bisulphide by pushing frass into it with its head. After three hours the larva was lying inactive at the bottom of the tube, and death followed soon after.

The studies on the life-history and control of this insect were commenced in April 1927 and carried on for a period of approximately two and a half years.

The writer is greatly indebted to the Government Entomologist, Mr. G. E. Bodkin, for the photographs which illustrate this paper and for reading through the manuscript.

References.

1. Beeson, C. F. C. 1920. Breeding cages and general insectary technique for woodborers.—Proc. 3rd Entom. Meeting Pusa 1919, iii, pp. 892–895, 2 pls.
2. Buxton, P. A. 1924. Applied Entomology in Palestine, being a report to the Palestine Government.—Bull. Ent. Res., xiv, pp. 289–338.



Fig. 1.

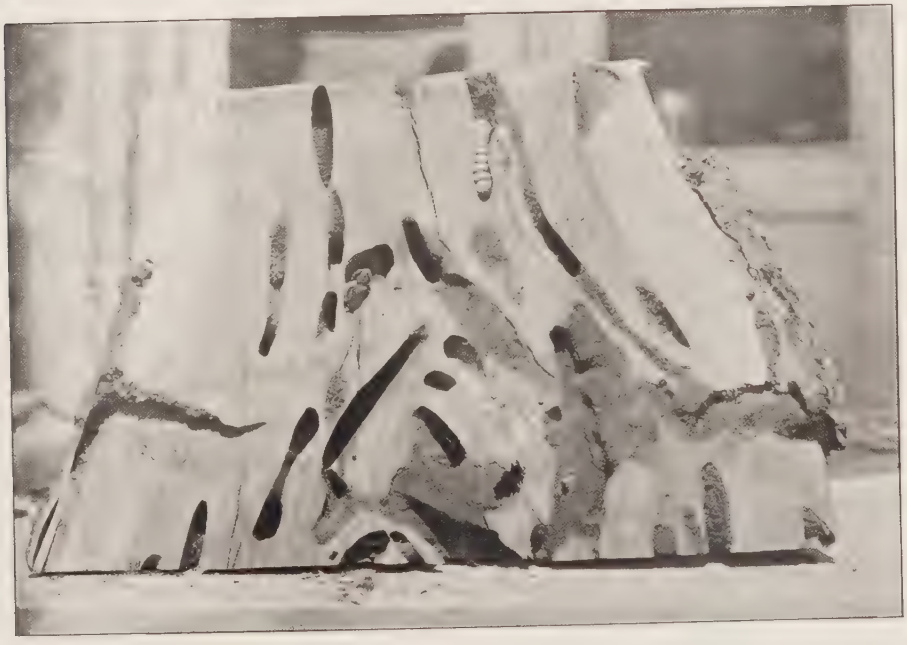


Fig. 2.

Fig. 1. Eggs of *Cerambyx dux* on bark of almond.
Fig. 2. Vertical section of almond log showing borings of larvae of *C. dux*.

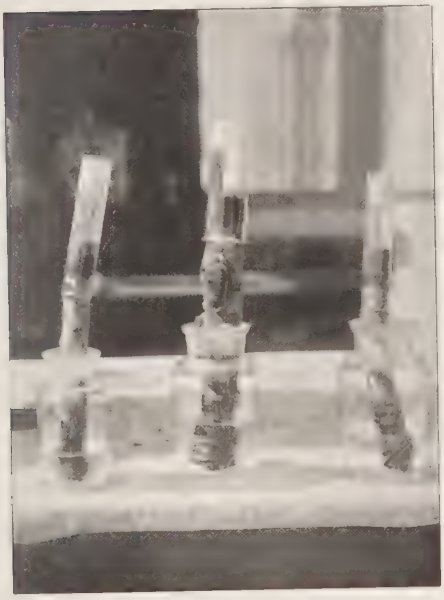


Fig. 1. Method of breeding larvae of *Cerambyx dux*.



Fig. 2. *C. dux*, in pupal cell

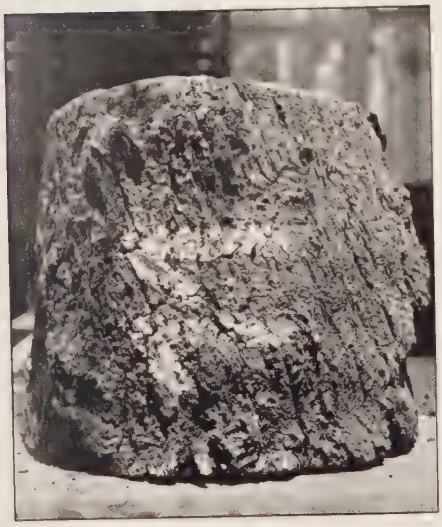


Fig. 3. Almond log attacked by larvae of *C. dux*, prior to removal of bark.

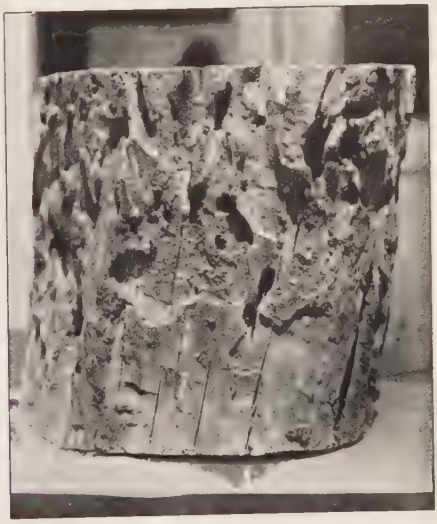


Fig. 4. The same log after removal of bark, with the borings exposed.

THE ORIGINAL HABITAT AND HOSTS OF THREE MAJOR SUGAR-CANE PESTS OF TROPICAL AMERICA (*DIATRAEA*, *CASTNIA* AND *TOMASPIS*).

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(Plate XIII.)

1. Introduction.

In a recent preliminary report (Myers, 1931) to the Empire Marketing Board on an investigation into the biological control of West Indian insect pests, I stressed a new theoretical consideration which has been more or less implied in the recognised technique of biological control work. It is well known that the greatest successes of biological control have been achieved by the introduction of an insect's natural enemies into countries which it has reached without them. The search for parasites has therefore been prosecuted where possible in the original home of the insect concerned. But if we desire not only to find promising parasites but also to discover any other limiting factors, the absence of which in agricultural areas may have led to the insect's outbreak as a pest—if, in short, with a view to exploring all possibilities of biological and cultural control we wish to discover why the insect has become a pest, it seems to me that we must be ecologically more fundamental. We must examine the status of the insect in an entirely primitive environment, in a virgin plant-association, and try to evaluate its position under an older and more stable balance than that of the cultivated areas. Thus in the present investigation in tropical America the primitive environment of a pest insect has been regarded not only as the most promising source of efficient parasites, but also as the key to its present status and eventual control. Unfortunately, however, there is no De Candolle to point out the home of the main pests, and the original habitat of the small moth-borers (*Diatraea* spp.), the giant moth-borer (*Castnia licoides*) and the froghopper (*Tomaspis saccharina*), three of the most serious insect enemies of sugar-cane in the New World, was unknown until the present investigation. Even the fairly legitimate assumption that the original host-plant would at least belong to the same family as its main cultivated host proved baseless in the case of *Castnia*.

The present paper incorporates a mass of data accumulated since the above report was written and summarises the present position of our knowledge. It should be followed by an account of the many new predators and parasites found attacking the pests concerned in their original habitats, but this must await their determination and description by systematic specialists.

In the identification of plants I gratefully acknowledge ready help from Kew in the case of certain critical species, in Haiti from Dr. H. D. Barker, in Santo Domingo from the late Dr. Ekman, whose tragic death has deprived tropical botany of one of its ablest systematists, in Trinidad from Mr. W. E. Broadway and Mr. R. O. Williams, and in Venezuela from Dr. H. Pittier. The bulk of the determinations have, however, been made by myself, and any errors are my own.

For generous assistance and facilities of every kind we are indebted to Mr. J. R. C. Gordon, Manager of Plantation Waterloo, Dutch Guiana; to Sir Edward Davson, Mr. C. Farrar, attorney for Messrs. Davsons, Ltd., Mr. Eccles, Manager of Plantation Blairmont, in Berbice; to Professor the Hon. J. S. Dash, Director of Agriculture,

and his staff, especially Mr. L. D. Cleare, Government Entomologist, in Demerara; and we owe very much to Mr. A. W. B. Long, Commissioner of the North West District.

In Venezuela our work was greatly facilitated by Mr. W. E. O'Reilly, British Minister at Caracas, and through him we are indebted to General Juan Vicente Gomez, Commander-in-Chief of the Army, to Dr. R. Requena, President of the Estate of Aragua, General Yañes, Jefe Civil of Ocumare de la Costa, Dr. Pacannis, of Central Tacarigua, Señor R. Dolge and Don Enriquez Eraso. We were helped greatly also by Dr. Henry Pittier, Director of the Commercial Museum of Caracas, Señor C. Vicentini, Treasurer of Venezuela, Dr. Eduardo Röhl, Manager of the Cervecería Aguila, and Coronel Ramon Peñas, Commandant at Carupaño. In the Delta of the Orinoco our best thanks are due to the Fathers of the Mission at Wausa, and to Señor Mariano Medina.

In Haiti, on my second visit, Mr. J. H. Magowan, O.B.E., British Chargé d'Affaires, did everything in his power, both officially and personally, to further my work. I received also very great help from Drs. Colvin, Barker, Boughton and Dozier, and Messrs. Hebert, Leonard and Dardeau, all of the Service Technique de l'Agriculture. For transport facilities by aeroplane and boat and for personal hospitality I owe much to the U.S. Marine Corps, in the persons of Major Sullivan, Major Davis and Lieutenant Walker, and to the Garde d'Haiti, especially Captains Aarons, Whitney and André, and Lieutenant Dietz. Monsieur André Chevallier was also kind and helpful.

In Trinidad and Antigua the co-operation of Mr. H. E. Box has been pleasant and stimulating.

To my wife I am indebted for constant assistance and for the photographs illustrating this paper.

Although the sugar-cane Diatraeas and the cane froghopper attack also a large variety of other grasses, it would be unjustifiable to consider them in any degree indiscriminate feeders. Nor is it ever safe to prophesy, on the basis of vegetative characters or floristic relationship, that this or that grass will be bored or sucked by these insects. Borers, for instance, will be found at times in grasses which seem absurdly thin, while stouter, more succulent species are neglected. Unquestionably of much greater importance than the characters of the individual grass species are the ecological factors dominating the plant-associations in which the grasses in question habitually grow. Speaking broadly, the three types of insects under discussion certainly seem to be adapted rather to plant-associations than to plant-species.

The main plant-formations at low levels in the West Indies and adjacent mainland are forest and savannah, including wet savannah, which merges into swamp. Forest associations vary from dry thorn-forest or scrub to heavy rain-forest. One general result of the present enquiry has been extremely surprising, namely, the discovery that several of the major sugar-cane pests were almost certainly originally forest species. To explain this in the report above cited I suggested that possibly the microclimate at the base of tall canes has more in common with that of a forest-floor than that of open grass-land. Pickles (1931) has since very suggestively developed this comparison further.

2. The Small Moth-borers (Diatraea spp.).

No fewer than 48 species of *Diatraea* are listed from the Americas in Box's excellent recent revision (1931). They are indigenous, and supplied the first recorded pests of sugar-cane after its introduction into the New World. All those of which the habits are known are practically confined to grasses. I believe the few records of Cyperaceous hosts need confirmation.

It was previously stated (1931 Report) that " in no single case has *Diatraea* been found in a virgin plant-association. We are as yet largely uncertain as to its original grass-hosts." Chiefly from explorations carried out since, it is now possible to discuss the provenience of five species, namely *Diatraea saccharalis*, *D. canella*, *D. impersonatella*, *D. busckella* and *D. bellifactella*. The first four of these are the major cane species in the West Indies and the adjacent mainland. *D. bellifactella* is not, at present, of economic importance. The case of a sixth species, *D. lineolata*, is very curious. Box (*l.c.*) has shown that this, which occurs in parts of Central America, the West Indies and northern South America, is, next to *D. saccharalis*, the most widespread of the American forms. It is practically confined to maize, there being only an exceptional record from sugar-cane in Cuba (Van Dine).* No wild hosts have been recorded, and it seems highly probable that the insect was primitively attached to maize and accompanied it into cultivation in the original home of the plant, which according to the available evidence (De Candolle, Burtt-Davy) was either the plateaux of Colombia or more probably of Mexico. Wild maize is believed not to exist, though Boturini Benaduci claimed to have discovered a wild race in Mexico about 1740 (see Nuttall, 1929). It would be of extreme interest to ascertain whether *Diatraea lineolata* attacks teosinte (*Euchlaena mexicana*), which is related somewhat distantly to maize and will hybridise with it. Since maize under cultivation spread by slow degrees till it reached Canada in the north and southern Argentina in the south, while the range of *D. lineolata* is in comparison still very limited, we have here a case of a host-plant much more adaptable than its pest insect.

Diatraea in the Antilles.

During the earlier visits the wild host-plants of *D. saccharalis*, the most widespread and most destructive of the New World species, were studied in Cuba, Haiti, Santo Domingo, Jamaica, and the Leeward and Windward Islands. Plank (1929) has also given the question considerable attention in Cuba. As a summary has already been given in the preliminary report, it will be necessary here merely to state that in no case, in the area in question, was *Diatraea* found in wild grasses at a distance from cane-fields. In every case it seemed more than probable that the grasses had been infested from the cane and not *vice versa*. Plank's list (*l.c.*) consists solely of grasses " that commonly grow in or near cane fields." I can add *Paspalum virgatum* and *P. densum*, which, under Cuban conditions, frequently grow at a distance from cane-fields; but two considerations militate against their being considered original hosts—firstly, their infestation varies inversely as the distance from the nearest sugar-cane, and secondly, although they are common hosts of other species of *Diatraea* in Trinidad and the adjacent mainland, they are never, in my experience, attacked by *D. saccharalis* there.

In view of all this, one might have suspected that *D. saccharalis* is not indigenous in the Antilles, but was introduced from the mainland. If such were the case, it certainly bears all the marks of very long establishment in Cuba. But against such a theory was its possession of an endemic (Greater Antillean) parasite, *Lixophaga diatraeae*, which, in spite of several years' work by Van Dine, Loftin, Plank, Box, Scaramuzza, myself and others, has not been found to attack any other host. Moreover, an aquatic grass, *Hymenachne amplexicaulis*, which, as we shall see later, is undoubtedly one of the original hosts on the mainland, was recorded by Jones as a host in Porto Rico, although in Cuba I searched it in vain. Another mainland host-grass, *Paspalum repens*, is reported by Chase from several localities in Jamaica, but has not been examined for *Diatraea*. It seemed probable, therefore, that *D. saccharalis* is indigenous at least in the Greater Antilles, but that its original hosts have been much decreased by cultivation, so that it is now primarily dependent on sugar-cane.

* Dr. Van Dine writes (8th January 1932) that this record was an error.—J. G. M.

Such was the state of our knowledge when in June 1931 I visited Haiti for the second time. In the course of other work I was able to pay some attention to *Diatraea*. I found it even rarer than before in the vicinity of Port-au-Prince and in the Southern Peninsula, and I failed to find an infestation in rice. A search in aquatic grasses on the Etang Miragoâne, the largest freshwater lake in Haiti, showed however, in August, an abundance of *Diatraea saccharalis* under conditions which are undoubtedly primitive. Adjacent patches of peasant canes and maize, even some which had been inundated by floods and were investigated from a canoe, were free from infestation. It was far out in the lake itself, in water of varying but considerable depth that the borers occurred, in great beds of floating grasses. Here were present also the two important larval parasites, *Lixophaga diatraeae* and *Microdus stigmaterus*.

The two chief host-grasses, each growing practically pure, and forming huge masses of floating vegetation, were *Hymenachne amplexicaulis* and *Luziola spruceana*. These two grasses, and *Eleocharis geniculata*, formed the bulk of the plants growing in the deeper water. There was distinct segregation of the three species, the *Eleocharis* growing furthest from the shore and the *Luziola* next. Mixed with the grasses were scattered, often numerous, plants of *Polygonum* (near *hydropiper*) and a large pink-flowered *Hibiscus* with red, prickly stems. Of interest and importance in the borer complex was the fact that grebes (*Podilymbus podiceps antillarum*) were very common and were building their floating nests either in open water or in the less dense beds of *Eleocharis*. On their old nests *Luziola* was germinating, and forming new colonies, extending its range thus into deeper water.

It has been remarked that pupae of *Diatraea* were on no occasion found in aquatic grass-hosts on the mainland of South America. In this connection it is interesting that in the small collection which time allowed on the Etang Miragoâne, one pupa was found in *Luziola*, and duly produced a moth. One larva of *Diatraea saccharalis* was found in a third water-grass, *Panicum geminatum*, which represents a new host-record.

There thus remains small doubt that *Diatraea saccharalis* is indigenous in the Greater Antilles, where it subsisted originally on aquatic grasses and thus must have been very much more restricted in distribution than it has since become under agricultural conditions. It is significant, as indicating the borers' predilection for aquatic grasses, that none of the numerous species of the swampy and inundated margins of the lake were infested.

In St. Lucia *D. saccharalis* is common in *Paspalum virgatum* on the edges of roads and cane-fields. I failed to find it in beds of the related *Paspalum millegrana*, growing far from cane and under virgin conditions, on the windward coast. There are, however, no endemic parasites of *Diatraea saccharalis* in St. Lucia, and no real indication that it is indigenous there.

In the damper valleys of the hills near Vieux Fort, in the southwest of St. Lucia, though not at Vieux Fort itself, another species, *D. canella*, occurs in sugar-cane—reaching here its northern limit. When the preliminary report was written it was not known north of Grenada, but Mr. Box has discovered it in St. Vincent. There are no data to indicate its original status in St. Lucia, St. Vincent or Grenada.

Diatraea in Trinidad.

Trinidad conditions afford us a transition to those of the mainland, of which, in fact, they are an epitome. As indicated in the preliminary report, *D. saccharalis* is only third in economic importance among the local species. It is the most widespread, but the least plentiful species in sugar-cane. The most abundant is undoubtedly *D. impersonatella*, and next to that, *D. canella*.

Most of the main plant-associations of Trinidad have been searched for their wild host-plants. Scrub and forest stations have so far yielded no sign of the cane

species. The natural grasslands of the Colony have been specially searched for these and froghoppers. They consist chiefly of two large swamps, the Caroni on the west and the Nariva on the east, and a line of savannahs extending eastward from the former swamp under the lee of the Northern Range.

The Caroni swamp has been considerably altered by partial drainage and periodic burning. West of the outermost longitudinal canal it consists almost solely of mangrove associations. East of this canal there are first dense beds of *Cyperus articulatus* and some *Eleocharis mutata*, followed by still wider beds of Pará grass, *Panicum barbinode*, regularly cut for fodder. Damper spots, and the banks of ditches and the Caroni River are densely clothed with *Hymenachne amplexicaulis*, while drier areas show a mixture of *Bactris* palms, a few bushes and small beds of *Heliconia psittacorum* and *Paspalum fasciculatum*. In places the stretches of Pará give place to considerable areas of *Thalis geniculata*, edged in some cases with high *Cyperus elatus* and *Canna* sp. A small patch of *Bactris* swamp-forest, with *Erythrina glauca*, *Spondias lutea* and other trees is bordered widely by *Paspalum densum*. One passes thence to scattered rice-fields interspersed with large patches of *Paspalum densum*, of *Paspalum conjugatum*, of *Ipomoea* sp., and Pará grass. *Diatraea saccharalis* has not been found in the swamp, not even in the *Hymenachne*, which is one of its mainland hosts. The *Paspalum densum* was lightly infested by *Diatraea canella* and the *P. fasciculatum* by *D. impersonatella*. We have seen in the preliminary report that this grass is the favourite host of *D. impersonatella*. It is, however, by no means certain that *P. fasciculatum* is an original constituent of the Caroni flora. It may well have been an intruder following on partial drainage. I have nowhere in Trinidad seen it under definitely virgin conditions. As a cane-trace and roadside weed it is widely distributed throughout the island.

The *Paspalum densum*, harbouring *D. canella*, is more likely to be primitive, and it may well have been one of the original hosts of *D. canella*. The favourite food of the latter, is, however, *P. virgatum*, which grows as a weed in a variety of situations throughout Trinidad, but never under indubitably virgin conditions. On portions of the east (*e.g.* Balandra) and south-east (*e.g.* Mayaro Bay) coasts *D. canella* occurs in two grasses which grow commonly in patches just above reach of the highest tides. One of these forms prostrate tufts, while the other, though stouter and erect, is clothed in every part with a pale bluish bloom. In floral characters both agree exactly with *Paspalum millegrana*, which is a favourite weed-host of *D. canella* about British Guiana cane-fields, and this identification has been confirmed by Mr. R. O. Williams; but superficially the plants look very different. In these essentially sea-coast grasses and in the swamp-dwelling though by no means aquatic *P. densum*, we doubtless see the original hosts of *Diatraea canella* in Trinidad. On the mainland it has so far not been found in any virgin association.

The Trinidad savannahs, under the lee of the Northern Range, are entirely edaphic in origin. The soils, according to Hardy, "consist of greyish white sand varying in depth from one to four feet—underlaid by a more or less clayey substratum of a mottled red, orange, grey and brown appearance." They "appear to be the much-leached residues of previously deposited material." The hummocky surface is water-logged during the rainy season and unduly dry at other times. By their vegetation these savannahs may be divided into two main types, the one probably related to the upland savannahs of the British Guiana-Brazil-Venezuela boundary and the other strongly reminiscent of the "wet savannahs" of British Guiana and the Orinoco Delta. The first kind, exemplified by the Piako (Piarco) and Mausica savannahs, show a dominance, save in wetter spots, of grasses over sedges, the abundant species being *Trachypogon plumosus*, *Paspalum pilosum* and *Thrasya robusta*. The first of these grasses is said to common on the upland savannahs of British Guiana. The woody vegetation is of the "orchard" type and consists very largely of *Byrsonima crassifolia* and *Curatella americana*. In other places cocorite palm

(*Maximiliana caribaea*) is easily dominant, the erect bush, *Coccoloba pubescens*, and an *Andropogon* are common, and large beds of *Heliconia psittacorum* appear. In wetter spots more sedges enter, and a few iris-like tufts of *Paspalum densum*. Small savannahs of similar appearance may be seen in the Northern Range itself between 1,000 and 1,500 feet. Here the dominant grass is usually either *Trachypogon plumosus* or *Thrasya robusta*—seldom a mixture: but a clambering sedge (a wide-leaved *Scleria*) and a coarse grass, *Axonopus equitans*, are often common, and the dominant shrubs, *Curatella* and *Byrsonima crassifolia*, are intermixed to a varying degree with other species.

The second main type of Trinidad savannah is exemplified by the southern part of the Aripo savannah and is characterised by a greater abundance and variety of sedges and by the presence of the highly characteristic moriche palms (*Mauritia setigera*) (Pl. xiii, fig. 1). These palms, with the other woody vegetation, tend to be segregated into islands standing out of the sea of sedges and grass, among which occur a number of interesting terrestrial orchids, bladderworts and sundews, and in places a straggling tangle of *Cassytha americana*. The smallest islets, of a few bushes only, consist almost invariably of *Clusia nemorosa* solely. In slightly larger patches *Moronobea coccinea* joins the company, and in drier parts, *Byrsonima crassifolia*. The large islands containing a variety of forest trees, are overtopped by *Mauritia* palms, seedlings of which spring up thickly from the undergrowth of breast-high sedges (coarse cutting species including a stout *Scleria*) interspersed with a few Melastomes. These larger islands are edged, as often in the Orinoco Delta wet savannah, almost continuously by fat-pork (*Chrysobalanus pellocarpus*) bushes.

It is remarkable that on none of these extensive grass-lands has any species of *Diatraea* yet been taken. Yet *D. saccharalis* occurs—very sparingly it is true—in an isolated field of sugar-cane situated in a patch of forest between the two main divisions of the Aripo savannah, while *D. canella* is not uncommon in roadside *Paspalum virgatum* within a few hundred yards of the other savannahs.

To sum up the Trinidad position, the only injurious *Diatraea* which has been found in a definitely primitive environment is *D. canella* in littoral *Paspalum millegrana*. The commonest wild hosts of *Diatraea* in Trinidad are *Paspalum fasciculatum* (*D. impersonatella*) and *P. virgatum* (*D. canella* and *D. impersonatella*), but these are almost solely weeds of the settled areas. It is curious that *D. saccharalis* has not yet been taken in a wild grass in Trinidad, either native or introduced. If, however, this species is indigenous both to the Greater Antilles and to the mainland, it is hardly likely that it is not also native here.

There remains in Trinidad one very extensive grass-association not mentioned in the above paragraphs. Cacao-plantations occupy a very considerable proportion of the island's area, and their commonest weed is probably the grass, *Chaetochloa sulcata*, which forms dense continuous beds unless assiduously eradicated. Until Mr. Box's recent visit, although a search had been made in the Moruga district, no *Diatraea* had been found in this grass. Mr. Box found it to be the host of the hitherto very rare *Diatraea* species, *D. bellifactella*, which has not yet proved a pest of any useful plant. He has found, moreover, that it is attacked by several interesting Braconid parasites, at least one of which does not parasitise the cane-borers. More recently I have found *Chaetochloa sulcata* on loose stream banks in virgin forest near the south coast, between Guayaguayare and Moruga. It was here attacked by *D. bellifactella*, thus establishing the primitive status of the species.

On cacao estates at the higher levels, *Ch. sulcata* is often mixed with some *Ch. palmifolia*, a much stouter species, which entirely replaces the former in Grenada. Since *D. bellifactella* has been recorded from the latter island (Box) it is probable that this is its host-plant, but a search of a few plants at an elevation of about 1,600 feet, near the Grand Etang, failed to reveal its larvae.

Diatraea in Dutch and British Guiana.

Some account of *Diatraea* in sugar-cane and weed-hosts in British Guiana has been supplied in the preliminary report. It remains to mention here the results of subsequent investigations in Venezuela and in more primitive Guiana environments.

In Nickerie, Dutch Guiana, the chief grasses known elsewhere to be *Diatraea*-hosts are *Paspalum virgatum* and *P. densum* in abandoned fields and *P. repens* with *Hymenachne amplexicaulis* in some of the trenches. Before the time of our visit the two former grasses had been almost entirely eradicated from the dams. Cane-field conditions and cultural practice are closely similar to those of British Guiana, and the chief borers obtained from cane "dead hearts" were predominantly *D. canella* and secondly *D. saccharalis*. An examination of three lots of canes of about 100 each, at the mill, showed a stalk infestation of 78·1, 93·3 and 89·7 per cent. respectively. The immediate hinterland behind the water conservation dam shows no indication of *Diatraea* breeding-grounds—a sea of *Typha* to the horizon, said to hold 18 inches of water in the wet season. Scattered in this sea are occasional rounded copses of the large tree, *Erythrina glauca*—forming large islands—though not in the sense of occupying higher land, for the whole landscape is perfectly level.

In Berbice, British Guiana, an apparently undisturbed riparian grass-association, backed by rain-forest, was investigated on the Canje Creek, flowing into the Berbice River. Near the mouth of the creek the banks are, of course, fringed with mangroves. Further up, these are replaced by dense beds of gigantic *Montrichardia arborescens*, the haunt of numerous hoatzins (*Opisthocomus*). There were occasional floating islands of *Paspalum repens*. About ten miles from the mouth the vegetation again changes and the water is edged with a thick floating fringe of the grass, *Hymenachne amplexicaulis* mixed with some *Polygonum* sp., less *Eichhornia crassipes* and a yellow-flowered *Utricularia*, backed by *Montrichardia* and (or) *Drepanocarpus lunatus*. Behind this again is low rain-forest. The only other grass in the water or near the edge is firstly, *Paspalum repens*—only one small floating islet seen, pushed *up*stream by the tide; and secondly, *Echinochloa polystachya* scattered very infrequently in the *Hymenachne* fringe itself. *Diatraea saccharalis* was found in both the *Hymenachne* and the *Echinochloa*. It had been found in the latter nearly two years previously on Plantation Blairmont, but through absence of flowers, the grass was not then determinable. The other aquatic grass, *Paspalum repens*, is already well-known as a host for *D. saccharalis* in the trenches of the Guiana cane-lands. Since the lower ten miles of the Canje Creek are at no great distance from the cane-lands, it is uncertain whether the *Diatraea* population of these three aquatic grasses is really an indigenous one.

Diatraea in the Orinoco Delta.

There was no room for similar doubts in the Orinoco Delta, where we examined all the grass-associations we could find on the Amakura River and three of its tributaries, namely, the Yarikita River and the Carapo and Awaracaba Creeks.

The Orinoco Delta is a low-lying area of some 12,000 square miles with a general precipitation of certainly at least 100 inches, though unfortunately there are no records. It is biologically largely unknown. The following remarks must therefore be applied only to the southern part, in the region of the Amakura. The dominant plant-formation is swamp-forest chiefly of the type known in British Guiana as truli-swamp, and marked by the extreme abundance of the palms of that name (*Manicaria saccifera*). This vast expanse of wet forest, through which the rivers wander with no defined banks, is broken at rare intervals by low lateritic hills or lower sandy knolls, clothed with forests of taller trees, in which occur almost invariably either occupied clearings of Warrau Indians or patches of *Cecropia* and other secondary trees marking temporarily abandoned sites.

Even on the wet level country the swamp-forest is, however, not quite continuous, but is interrupted by the so-called "wet-savannahs" which vary from mere strips along the banks of creeks to seas of sedges ten miles across.

So far as the forest is concerned, both swamp-forest and that of the low hills, it may be said at once that *Diatraea* was never found in any of the less aquatic forest grasses, of which the most abundant are *Panicum* species of the *frondescens*, *stoloniferum* and *pilosum* type, and an *Axonopus*. We must revert to the forest associations when discussing the distribution of *Castnia* and *Tomaspis*. *Paspalum fasciculatum*, *P. virgatum* and *P. millegrana* seemed to be entirely absent, and with them *Diatraea impersonatella* and *D. canella*. Only *D. saccharalis*, which we have elsewhere given reasons to consider an originally semi-aquatic species, was found in the Delta.

The Amakura River at the junction of the Yarikita shows the usual bank fringe of a wide river, the view into the forest being obscured by a curtain of creepers. The dominant riparian trees are *Pachira aquatica* (one of the original hosts of the cocoa-beetle, *Stirastoma depressum*) and *Pterocarpus draco*. Mangroves (*Rhizophora mangle*) begin to appear about 12 miles down-river, but do not seriously challenge the dominance of the *Pachira-Pterocarpus* association until a few miles above the junction of the River Cuyuwini. In front of the forest-fringe are extensive beds of water-hyacinths (*Eichhornia azurea* and *E. crassipes*) and of a stout, luxuriant form of *Paspalum repens*,* sometimes mixed and sometimes separate. In mixed beds the *Paspalum* is usually fronted with a narrow fringe of hyacinths and backed by masses of the grass, *Sacciolepis striata*, joining it to the forest fringe itself.

The most noteworthy feature of the Amakura River is the large number of floating islands, large and small, which sail up and down with every tide. The basis of these islands consists usually of the two hyacinths, with a small *Salvinia* regularly covering the water-surface between their stems. Larger islands naturally often possess a more varied flora – the grass *Sacciolepis striata*, a *Commelyna* sp., a *Jussieua* sp., and a twining Legume. Occasionally *Paspalum repens* forms pure islands of its own. The large islands support an interesting fauna, including the spurwing (*Jacana jacana*), the reed-bird (*Donacobius atricapillus*) and numbers of aquatic grasshoppers.

Below the Awaracaba Creek the beds of *Paspalum repens* are replaced by similar ones of the much stouter *Panicum elephantipes*, which occurs also on the Aruka River and Koriabo Creek in the North-West District of British Guiana. It is usually associated with a mangrove fringe forest, while *P. repens* more often fronts *Pachira-Pterocarpus* higher up the rivers. A few miles up the Cuyuwini, however, from the Amakura, while still within the zone of dominance of mangroves, *P. repens* forms large beds, to the exclusion of the *Panicum*.

The beds of *Paspalum repens* and of *Panicum elephantipes* on the main river (Amakura) were assiduously searched for *Diatraea* without success. In the former, dead hearts caused by a Dipterous borer were not uncommon, and extensive patches were grazed flat by capybaras (chigüire), while in the *Panicum*, the central shoot was often killed by external feeding, probably by grasshoppers.

In the Yarikita River, however, near its junction with the Amakura, a large bed of *Paspalum repens* eventually yielded a considerable number of *Diatraea saccharalis* larvae, extensively parasitised by a *Microdus* sp. Since the Yarikita and the whole of the Amakura, so far as we saw it, traverse uninterrupted forest, we were anxious to investigate the savannahs of the Carapo and Awaracaba Creeks, both affluents of the Amakura left bank.

* This is one of the several kinds of floating grass known as "Missouri grass" in British Guiana. It is usually called "fine Missouri grass," but whether it is the undetermined *Panicum* mentioned by Schomburgh ("Travels in British Guiana," Roth's trans., ii, pp. 386–387) as alleged to have been introduced into the Demerara River from the Orinoco, I do not know. *Paspalum repens* was originally described from Surinam, and is presumably indigenous in the Guianas and Venezuela.

The mangroves of the main river extend scarcely a mile up the creek. In front of them a few beds of *Panicum elephantipes*, of *Hymenachne amplexicaulis*, and later, of *Paspalum repens* appear. Later still the only floating grass beds consist of *Sacciolepis striata*, a very fine-leaved sedge (not in flower), and a small grass with short broad blades, likewise not flowering. As the stream narrows it takes on more and more the character of a typical black-water creek, and the bank curtain disappears, so that undifferentiated truli swamp comes right to the water's edge.

The main savannah on the Carapo is not a large one. It is fringed with the usual aeta palms (*Mauritia flexuosa*) and is covered by one dominant coarse cutting sedge (*Rhynchospora* sp.) known in British territory as "savannah grass," growing to a height of six feet. Marking the passage of the creek, however, are wide stretches of *Sacciolepis striata* and the fine-leaved sedge, growing in deeper water, with considerable white *Polygonum*, *Eleocharis geniculata*, a clambering *Mikania* sp., and small beds of luxuriant *Hymenachne auriculata* and of *Panicum elephantipes*. These last were assiduously searched for *Diatraea* with no success whatever, and as similar results awaited our examination of the much more extensive Awaracaba savannah, it is probably safe to say that *Diatraea saccharalis* does not breed in wet savannah even when its host-grasses are present.

Continuing up the Carapo Creek through the savannah we entered forest again, and encountered large floating beds of *Hymenachne auriculata* along the banks, under dense forest shade, the trees practically meeting over the now narrow stream. Here *Diatraea saccharalis* was breeding. Similar and adjacent beds of *Hymenachne amplexicaulis* and *Sacciolepis striata* yielded none. All these beds were thickly infested with large electric eels (*Gymnotus*).

At three Venezuelan clearings in drained swamp forest, on the Amakura and the Cuyuwini, and at six aboriginal clearings (lateritic or sandy elevations) on the Yarikita, Amakura and Carapo, we made a close examination of the local sugar-cane. There are two varieties—a "white" and a "black," both apparently brought in long ago by the Warrau Indians to plant on their more or less temporary clearings. The larger areas of a few acres, grown at the Wausa Mission and at other points by Venezuelans, are identical and have been derived from the local Indians. As we shall see later these canes yielded us a rich haul of *Castnia* larvae, in collecting which we frequently cut out and split up whole patches of cane. *Yet not a sign of Diatraea was ever found*,* nor did the Indians, who are excellent observers, know of any other borer than *Castnia* and *Metamasius*. This is the more remarkable from the fact that throughout the West Indies and the adjacent mainland I have consistently found that, *other things (especially parasites) being equal*, the *Diatraea* infestation from estate to estate and from Colony to Colony, varies directly with the rainfall. This is, of course, in direct opposition to Wolcott's local findings in Porto Rico, which were however probably influenced by irrigation. My wife informs me that there is historical evidence that the Warrau have probably cultivated sugar-cane on these clearings in the Delta for at least two centuries.† Yet *Diatraea* has evidently not yet learned to attack it. This lends strong support to the view that one of the original habitats of *Diatraea saccharalis* is the floating grass-association along the smaller creeks of the Orinoco Delta.

Diatraea in Northern Venezuela.

Sugar-cane is grown fairly extensively in northern Venezuela. Our observations

* At the Wausa Mission, on the Amakura River, a considerable quantity of maize was also examined for *Diatraea*, with no success.

† Sugar-cane was planted at the mission of Rosa Blanca, near the mouth of the Barima River, by the Spanish priest, Ortega, about 1650. ("Misiones de Rosa Blanca y San Juan de las Galdonas (1656)," by Mateo Montalvo de Jarama. Printed from MS. in Biblioteca Municipal, Madrid. Published Madrid, n.d., pp. 150–255).

were largely confined to the valley of Caracas and the neighbourhood of Valencia. The large cane areas near Maracaibo were not visited. The former lies at an elevation of about 3,000 feet in the coastal Cordillera. The average annual rainfall (Sifontes, 1928) from 1920 to 1926 was 872·1 mm. (34·3 inches). The two main cane varieties are known locally as " Salangor " and " Criollo," the former being used for the manufacture of aguardiente and the latter for that of coarse loaf-sugar called *papelon*. Some of the earlier Javan varieties and B H 10 (12) are also coming into cultivation. Stalk infestation by *Diatraea*, as gauged by the few mill-counts we were able to make, varied from 23 to 88·2 per cent. At the time of our visit (December) it was exceedingly difficult to find any dead hearts among the young canes ; thus evidently there is a marked seasonal intermission in borer activity.

Of original host-grasses in the Caracas Valley there are apparently none, while the weed-hosts are rare, and include merely such forms as the introduced *Eleusine indica*. The same remarks apply to the cane cultivations in the great valley-plain of Valencia, where we were privileged to visit the Central Tacarigua, a large estate belonging to General Juan Vicente Gomez, situated at an elevation of about 1,700 feet. The average rainfall (Sifontes) is 39·9 inches at Valencia. There the chief cane is Cristalina (White Transparent) but considerable areas of B H 10 (12) and some Santa Cruz and Criollo are grown.

The chief cane-borers in both these localities, as already noticed by Box and later by Osborn, are *Diatraea busckella* and *D. canella*. I obtained one new moth-borer (not *Diatraea*) but no *D. saccharalis*.

Near La Guaira on the Caribbean littoral, conditions are exceedingly dry (rainfall 18·4 inches). Here in a small field almost on the shore I found a considerable infestation of *Diatraea busckella* alone. Alternate host-plants seemed entirely lacking.

Much further east, at Carúpano, conditions are encountered more similar to those of Trinidad. The rainfall is, however, still very low—only 30·0 inches. Here the predominant borer in young canes was *D. canella*, with an occasional *D. saccharalis* — the only larvae of this species I have found in cane in Venezuela. No alternate host-plants were observed.

Still on the Caribbean coast, but much further to the west, at Ocumare de la Costa, several large stands of the tall stout grass, *Panicum grande*, six to eight feet high, were found growing in the water at the edge of a stream, within five miles of the sea, but many miles from the nearest sugar-cane area. Here was an infestation of *Diatraea saccharalis*, unusually heavy for a wild host, and attacked at a high rate by several Braconid and Muscoid parasites. In this grass, as invariably in wild hosts, the *D. saccharalis* were high up in the stems, sometimes in the flowering culm itself, the internode below being full of water. The same grass occurs sparingly as a member of an induced association in roadside ditches at several Trinidad localities, where, however, it is apparently never infested by *D. saccharalis*. Mr. Box found in Trinidad examples of occasional larvae of *D. impersonatella* and *D. canella*.

Diatraea in the Venezuelan Llanos.

The llanos, those extensive level Venezuelan plains comparable only to the pampas of the farther south, were crossed from San Juan de los Morros to San Fernando de Apure, following almost exactly Humboldt's route. In spite of the fairly frequent descriptions of their limitless expanses and the dedication to them of more than one book (*e.g.* Sachs, Paez), their vegetation is largely unknown. I am publishing elsewhere a short sketch of their plant-covering. At the time of our crossing, in late December, they were so exceedingly dry that it was difficult to realise that in winter* they are largely under water.

* Contrary to the usage elsewhere, the rainy season in Venezuela is known as " winter " (*invierno*) and the dry season as summer (*verano*).

The llano vegetation proper is invaded along the banks of the numerous rivers by fringing woods, which Pittier classes as monsoon forest.

On the bank of one such river, the Guarico, near El Sombroro, a small patch of wild rice, *Oryza latifolia*, had indubitable *Diatraea* borings, probably due to *D. saccharalis*, and an empty *Microdus* cocoon.* This was in partly cleared land. In general the fringing forest sheltered no grasses suitable for *Diatraea* or froghopper, the silty soil between the trees being usually bare as a result of the annual inundations.

North of Camaguan, where the route south from Calabozo touches the large river Portuguesa, the plant-formations vary from open grassland, with scarcely a tree in sight, to close orchard types of savannah with a thick sprinkling of bushes and small trees, chiefly *Curatella americana*, *Byrsonima* (several spp.) and *Bowdichia virgilioides*. A dominant grass in the latter association is frequently *Cymbopogon condensatus*, while on the open areas there are long stretches of the reddish *Andropogon condensatus* and of *Sporobolus indicus*. A very abundant plant in all the drier associations is the strongly aromatic Labiate, *Hyptis suaveolens*, which is sometimes the dominant herb for miles, probably owing to selective grazing by the immense herds of cattle and troops of horses which roam the llanos and have unquestionably already profoundly modified the original vegetation. Over large areas the bushes and trees are replaced by numerous colonies of the beautiful llanera palm (*Copernicia tectorum*) (Pl. xiii, fig. 2). In damper spots lagoons still contained a little water and supported near their margins a scanty growth of *Thalia geniculata*, *Eleocharis geniculata* and *Cyperus articulatus*, with the grasses *Steirachne diandra* and *Sacciolepis vilfoides*, all save the *Thalia*, closely grazed, not only by semi-domestic stock, but also by deer and capybaras. Many of the lagoons are very widely bordered by almost pure stands of the erect, pink-flowered *Ipomoea crassicaulis*, probably another effect of selective grazing.

Further south the River Apure and its large tributary the Portuguesa are bordered to a width of many miles, by vast plains covered almost entirely, at the time of our visit, with one stout species of grass, whose close-ranked sterile culms reached in places a height of six feet. At the end of the rains these culms had evidently sprung up in the drying mud, from perennial stolons. It is locally known as "gamalote," a name given, as Chase has shown, to many large grasses in Latin-America (*e.g.*, Guinea grass in northern Venezuela, and *Chaetochloa sulcata* in Trinidad). No flowers were to be found at the time of our visit—nothing but sterile culms—and the species seems never to have been determined. I shall give reasons in a botanical publication for identifying it with *Paspalum fasciculatum*.

In this grass, especially on the recently bared silt a few yards from the water of the Apure River (and at similar spots on the Portuguesa), *Diatraea* larvae were by no means hard to find, boring in the higher internodes and causing characteristic and conspicuous dead hearts. By far the commonest species was *D. saccharalis*, but *D. impersonatella* and *D. busckella* were present also. Out of 198 larvae collected for dissection, 190 were the former species, six were *D. impersonatella* and two *D. busckella*. The latter two species were found further from the water, and it is my theory that *D. saccharalis*, with its already noted *penchant* for aquatic grasses, is the first to attack the soft new culms while the silt is yet wet. Thus it is found concentrated along the ever-receding water-line. The other species attack the older culms on the dried mud, which covers a much greater area at any one time and makes the search for borers more difficult.

It is curious that, as in *Paspalum repens*, no pupae whatever were found in *P. fasciculatum*.

* The same grass was searched at Ocumare de la Costa without success.

D. saccharalis occurred in two other grasses on the Apure River—namely, very abundantly in *Paspalum repens* on a small lagoon near San Fernando, and more sparingly in *Echinochloa polystachya*, of which a few plants were growing in front of a dense riverine stand of *Paspalum fasciculatum*.

The nearest sugar-cane areas are several hundred miles distant from San Fernando de Apure. Occasional small fields of cane occur, however, near houses on the llanos, and these consistently yielded no trace whatever of *Diatraea*. This was the less surprising in view of the prevailing drought; but the rainfall, which is sharply limited as to season, is, at San Fernando, 49·5 inches—thus considerably more than at Caracas. There can be no doubt whatever that the wide grassy plains of the Apure must be considered one of the original habitats of *D. saccharalis*, *D. busckella* and *D. impersonatella*.

List of wild Food-plants of Diatraea spp.

I leave to a compiler with better access to the literature the useful task of producing a complete catalogue of *Diatraea* food-plants. The following list is complete only for my own investigations, but it includes also a few available records from the same area. The latter are credited to the authorities concerned.* The division into original hosts and weed hosts is, I believe, fundamental, since in the first the infestation has proceeded from the grasses to the cane, while in the second the reverse has probably been the case. Some of the weed hosts, *e.g. Panicum barbinode*, are so rarely attacked that the records may be considered accidental in the fullest sense of the word.

DIATRAEA SACCHARALIS, Fabr.

Original hosts: *Paspalum repens*, *Paspalum fasciculatum*, *Panicum grande*, *Panicum elephantipes*, *Panicum geminatum*, *Echinochloa polystachya*, *Hymenachne auriculata*, *H. amplexicaulis*, *Oryza latifolia*, *Luziola spruceana*.

Weed hosts: *Valota insularis* (P.), *Leptochloa virgata* (P.), *L. mucronata* (H.H.L.), *Echinochloa colonum* (P.), *Eleusine indica* (P.), *Sorghum halepense* (P., and H.H.L.), *Tricholaena rosea* (P.), *Andropogon schaenanthus* (P.), *A. muricatus* (H.H.L.), *A. glomeratus* (J.B.), *Paspalum urvillei* (J.B., recorded as *P. larranague*), *P. virgatum*, *P. densum*, *Panicum gymnocarpon* (J.B.), *P. dichotomiflorum* (J.B.), *P. barbinode* (H.H.L.), *Axonopus capillaris* (Box), *Coix lachryma-jobi* (Box and myself).

DIATRAEA CANELLA, Hamps.

Original hosts: *Paspalum millegrana*, *P. densum*.

Weed hosts: *Paspalum virgatum*,† *Panicum grande* (Box).

DIATRAEA IMPERSONATELLA, Walk.

Original host: *Paspalum fasciculatum*.

Weed hosts: *Panicum grande* (Box), *Paspalum virgatum*, *P. millegrana*.

DIATRAEA BUSCKELLA, Dyar & Heinr.

Original host: *Paspalum fasciculatum*.

DIATRAEA BELLIFACTELLA, Dyar.

Original host: *Chaetochloa sulcata*.

3. The Large Moth-borer (Castnia licoides).

An account of the earlier economic history of this pest, and of the investigations up to the discovery by my wife of its wild food-plant in British Guiana, has already been presented in the preliminary report and need not be repeated here.

* "H. H. L." signifies Holloway, Haley and Loftin; "P." Plank; and J. B., Jones and Bradley.

† *P. virgatum* may very probably prove to be one of the original hosts, but I have never yet seen it in a virgin association. It was originally described from Jamaica, but is now widespread as a weed and roadside grass.

Following the knowledge that *Castnia* occurred in the Musaceous plant, *Heliconia Bihai*, in the North-West District of British Guiana, we made a further study of it there and in the Delta during February and March, 1931. An immediate result was the discovery of a Tachinid parasite attacking the larvae, and giving every promise of utility if it can be established in the Trinidad cane-fields.

Besides *H. Bihai*, several other species of *Heliconia*, and notably *H. humilis*, occur commonly in the forests of Trinidad and the adjacent mainland. Neither these nor the savannah species, *Heliconia psittacorum*, already described earlier in this paper, have so far yielded any *Castnia*.

There seems no doubt that *Castnia licoides* is essentially a forest species, and there is considerable evidence that it was in the Delta of the Orinoco that it first learned to attack sugar-cane. We have adverted already to the aboriginal clearings on small elevations rising out of the swamp-forest. There they have cultivated for a long period a variety of crops comprising firstly cassava, but also usually sugar-cane and plantains. In practically every clearing examined both these latter plants were heavily infested with this borer, and it is in the neighbourhood of these tiny settlements that edaphic and other conditions, as we shall see, favour an abundance of *Heliconia Bihai*.

In the virgin swamp-forest, whether of the truli (*Manicaria*) type or marked by a dominance of stilt-rooted Dicotyledonous trees, *H. Bihai* occurs as single plants at very rare intervals. It is, in fact, never abundant in virgin forest of any kind, but is largely a constituent of secondary growth, especially on the little oases of lateritic and sandy soils, more especially the former. As we have seen, these islands have practically all been occupied at some time or another by aboriginal families, and those which are not at present actually occupied are covered with secondary forest of various ages. Here *Heliconia Bihai* flourishes, and is, in fact, regarded by the Indians as an indicator of good soil, and it was on the largest of these lateritic outcrops, the Mabaruma hills, that we finally established at Wanaina a collecting base for *Castnia* parasites.

On these hills exists every transition between clearings under cultivation and very old second-growth forest with tall trees. In the younger formations *Heliconia Bihai* frequently forms dense luxuriant stands to the exclusion of every other plant save an occasional *Cecropia* (Pl. xiii, fig. 3). In such "reefs" the plants are sometimes twenty feet high. *Cecropia* is among the first to invade these close stands, and very soon overtops them. It is joined by *Inga* spp., *Didymopanax morototoni*, *Pentaclethra filamentosa* and even silk-cottons (*Ceiba pentandra*) drawn up to tall, thin poles by the shade of the rapidly-growing *Cecropia*. In these circumstances the stands of *Bihai* gradually thin out, and there is considerable space between their clumps. This space is colonised by the shade-tolerant trees of a later succession, and the result is soon tall secondary forest with only scattered clumps of *Bihai* (Pl. xiii, fig. 4).

Now it has long been a dictum of economic entomology that one of the factors producing serious insect infestations in colonial and tropical crops is the more or less sudden clearance of large areas of mixed forest or other indigenous association and their substitution by an equally wide expanse of one cultivated species, such as sugar-cane. This is said to offer unlimited opportunities to the insects attached to that plant or to any native ones which may learn to attack it. There is considerable evidence for this view, and the present investigation has certainly found that peasant crops, especially sugar-cane, are usually much less infested by the current insect pests than are estate crops. But the distribution of *Castnia licoides* in *Heliconia Bihai* does not support the theory. We should expect that the dense reefs of this plant would prove the best collecting ground, and my Indians acted for several days on this assumption. We found eventually that the reverse was the case and that, in spite of the fact that in the reefs the men were cutting the whole

time and thus examining at least four times as many plants in the day, they obtained on the average exactly three times as many *Castnia* larvae when they were working in older secondary forest where the clumps of *Bihai* were scattered. I offer no explanation of this, but may remark that the adult insect is by no means a shade-lover.

In Trinidad also, *Castnia licoides* attacks *Bihai* in second-growth forest. It occurs up to an elevation of at least 2,000 feet. I have taken the larvae also in *Paspalum virgatum*, once in a cane-field trace, and once in a small clearing in virgin forest between Guayaguayare and Moruga.

In Venezuela we found one larva boring sugar-cane in the valley of Caracas.

4. The Cane Froghopper (Tomaspis saccharina, Dist.).

Since my preliminary report was written, in which it was suggested that the sugar-cane froghopper is a forest insect, Pickles (1931) has published a very suggestive resumé of the evidence for this theory. Earlier in the present paper is a brief ecological sketch of the main swamp and savannah associations which have been searched in vain for froghopper in Trinidad. The most striking case is that of the Mausica Savannah, where the road is continuously bordered by short grasses. There, at the beginning of March 1930, I used a sweeping-net along the road until this left the savannah and entered the rain-forest. One hour's sweeping before it came to the forest yielded not a single froghopper; the first sweep within the shade of the latter produced five.

Tomaspis saccharina does not occur on the mainland, but a very closely related species, *T. bodkini*, Williams,* was recently studied in the Orinoco Delta and the North-West District, British Guiana. It occurred commonly on some, but by no means all, of the elevated aboriginal clearings mentioned, chiefly on the sandy knolls. There, in the space around the Indian huts, were grassy patches containing *Paspalum conjugatum*, *Syntherisma digitata*, *Panicum pilosum* and occasionally a small, fine-leaved *Cyperus*. *P. conjugatum* was dominant, and was the preferred host of *T. bodkini*, which also occurred, however, on the *Syntherisma*. *Tomaspis pubescens*, Fabr., was usually present in the same company, but nearly exclusively on the *Paspalum* and the small *Cyperus*.

No froghoppers were found in the wet savannahs of the Orinoco Delta, nor on the llanos of Venezuela.

With reference to froghopper habitats in Cuba, the grass referred to as *Paspalum distichum* in my preliminary report (E.M.B.42) is really *P. notatum*.

5. Summary.

A study has been made of the small moth-borers (*Diatraea*), the giant moth-borer (*Castnia*), and the froghopper (*Tomaspis*) of sugar-cane, in their respective primitive environments, primarily with a view to finding new parasites for them and secondarily to obtain light on their ecology under agricultural conditions.

The original hosts of *Diatraea saccharalis* are shown to be certain aquatic and semi-aquatic grasses growing at the edge of forest creeks in the Orinoco Delta and of rivers flowing through the Venezuelan llanos, and in lakes of the Greater Antilles.

In the llano habitat *D. busckella* and *D. impersonatella* were found under indubitably primitive conditions.

The original host of *D. canella*, another destructive cane species include two forms of *Paspalum millegrana*, growing on the Trinidad littoral.

* Williams first published this species with a coloured plate, but no description, Mr. Pickles has now published a formal description and a competent comparison with other species (Stylops, i, 1932, p. 14).

Castnia licoides is attached to the Musaceous plant, *Heliconia Bihai*, in the forests of Trinidad, the Orinoco Delta and North-West British Guiana. It is much more abundant in scattered clumps growing in high forest than in solid "reefs" of the host-plant in more recent clearings.

The Trinidad froghopper is shown definitely to be originally a forest insect.

The Trinidad swamps and savannahs are found to afford no breeding-ground to any of the three major cane pests discussed.

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Explanation of Plate XIII.

Fig 1. Aripo Savannah, Trinidad. Southern part, showing "island" dominated by aeta palms. (*Maurilia.*)

,, 2. Llanos, State of Guarico, Venezuela. Palms, *Copernicia tectorum*

,, 3. Secondary rain forest, North West District, British Guiana Dense reef of *Heliconia Bihai* (cut).

,, 4. Secondary rain forest, North West District, British Guiana. Scattered *Heliconia Bihai* in older forest. The hat marks a height of 6 feet.



Fig. 2.



Fig. 4.



Fig. 1.



Fig. 3.

ECOLOGICAL STUDIES ON THE MOROCCAN LOCUST IN WESTERN ANATOLIA.

By B. P. Uvarov,

Imperial Institute of Entomology.

(Map.)

Introduction.

The present paper is the outcome of a visit to Turkey at the invitation of the Turkish Government in the summer of 1931 to study the local locust problem and to advise on the general policy of locust control.

Of the two species of locusts active in Turkey, one, the Desert Locust (*Schistocerca gregaria*, Forsk.), breeds normally well beyond the boundaries of the State, and it is only during exceptionally serious outbreaks that swarms of this species invade south-eastern and eastern vilayets, as was the case in 1929–1930. The other species, the Moroccan locust (*Dociostaurus maroccanus*, Thnb.) is, on the contrary, indigenous in Turkey, and certain areas are in constant danger from its invasions. Studies of the Moroccan locust constituted the main aim of my voyage, which took place during the month of July and the first half of August. The period was very unfavourable for the investigation, since it was much too late to observe any oviposition, and only scattered adults were found in some places; moreover, ecological studies on the vegetation of egg-laying places were difficult because most of the plants were by this time completely dried up by the sun, or exterminated by domestic animals. The results are, therefore, necessarily incomplete, and the conclusions reached must be regarded as only preliminary in character. However, they enabled me to form a definite general idea as to the distribution, ecology and epidemiology of the Moroccan locust in Asia Minor, and these data may be of interest for entomologists in other areas subject to invasions by that locust.

I should like to express my gratitude to the Government of the Turkish Republic for giving me an opportunity to carry out these investigations, and for the perfect local arrangements which greatly facilitated my work. I am also grateful to the authorities of the Imperial Institute of Entomology for granting me a leave of absence for this visit. It is a pleasant duty to express my sincere thanks to those who have helped me while in Turkey: to my friend M. Sureya Bey Effendi, on whose initiative my visit was arranged; to Atif Bey Effendi, Secretary of State for Agriculture; to Tevfik Bey Effendi, Director-General of Agriculture; to Nihat Shevket Bey, Director of the Burnova Institute for Plant Protection, who accompanied me on all my travels in Western Anatolia; and to numerous local officials, particularly to Haidar Bey of Demirchi, and Fuat Bey of Tireh, who spared no efforts to help me in my investigations.

Distribution of the Moroccan Locust in Asia Minor.

The area in which the occurrence of *Dociostaurus maroccanus* is possible appears to be very wide and to comprise practically the whole of Asia Minor. Indeed, the only part in which the species definitely does not occur is in the very humid zone along the Black Sea coast, and on the higher mountains; otherwise it has been found from the plains of the Mediterranean littoral to the high steppes of the inner plateau. There is no doubt that future faunistic studies will help to define the general area of its distribution more exactly, but this is a matter of relatively small

practical importance. All swarming locusts are known to occur in the solitary phase in an area very much wider than the regions where they may swarm and become injurious. This general rule obviously holds good for the Moroccan locust, since isolated individuals found by me in various places belonged to the short-winged solitary phase.

Invasion Areas.

Two main regions of Turkey are subject to periodic invasions of the locust (fig. 1). One comprises partly, or wholly, the vilayets of Urfa, Mardin, Diarbekir, Sirt and Marash, situated in the south-east of the Republic. This area represents only a part of a much greater area extending into the adjoining parts of Syria, Iraq and, probably, Persia. Unfortunately, my visit to Turkey took place in a season which was too late for this southern area, and I did not extend my investigations to it, although economically it appears to be more important than the second invasion area.



Fig. 1. Map of Asia Minor, showing the areas (dotted) subject to invasions by the Moroccan locust.

This second area occupies the whole western extremity of the peninsula, west from the line Eskishehir, Kutahya, Afyon-Karahissar, Beychehir, Adalia. It is a rich and densely populated country, and in the last outbreak, during the Great War, practically the whole of it was overrun by locusts for a series of years, and enormous damage was done.

It would, however, be incorrect to regard the whole of this large area as of equal importance in regard to the locust problem. It is a well-established fact that within the area subject to invasions by various locusts there are certain definite localities in which the locusts find the conditions suitable for the production of the swarming phase. In such localities the insects survive in sufficient numbers even during the years of minimum, when there are no swarms present, and from these localities new invasions start again. It was obviously a point of great theoretical and practical value to locate such *reservations* and to study their ecological conditions. The name reservations appears more suitable for these localities, since the term " permanent breeding-places " commonly used to designate them implies that the locust cannot breed permanently elsewhere. There is no doubt that in the case of the Moroccan locust, permanent breeding takes place over the whole area of its specific distribution, while there must be a limited number of reservations, characterised by some definite ecological conditions, where the swarming phase can arise.

A discovery of reservations represents obviously the first step in the direction of a comprehensive anti-locust policy aiming at the prevention of outbreaks, and my work was, therefore, concentrated on this particular problem.

From this point of view, my visit to Western Anatolia took place at a very favourable time. The Moroccan locust, after the terrible outbreak of 1910-1918, entered a long period of minimum and is at present concentrated in its reservations. The problem of locating the reservations and of studying their ecology has now been investigated with considerable success, though it remains far from being solved in all details.

Reservations.

Locust reservations, as a source from which invasions spread out, can be located with a considerable degree of certainty if the history of several cycles of outbreaks is known in detail, *i.e.*, if the oviposition grounds are carefully observed and mapped



Fig. 2. Map of Western Anatolia, showing the gradual spread of locust swarms during the last great outbreak, 1909–1918 (after Bücher ; re-drawn).

each year, particularly when the locusts are not numerous and do not present any danger. My first thought on arriving in Turkey was, therefore, to obtain information of this kind extending as far back as possible. Unfortunately, it appeared that insufficient attention has been paid to this highly important work in the past, and exact sketch-maps of the oviposition grounds were found only in two places (Demirchi and Kula). In other districts it was possible to obtain only very vague general indications, almost useless for the purpose.

The only definite indication as to where the search for reservations should be directed was obtained from the brief outline of the last serious outbreak during

the Great War, when an effective campaign was waged against locusts in Anatolia by German specialists (Bücher, 1918). So far as it has been possible to ascertain, the outbreak began in 1909 in the neighbourhood of Takmak (or Eshme) and Kula, in the north-east of the Manisa province. During the subsequent years a gradual spread of swarms took place (see fig. 2) until in 1917 the whole of western Anatolia was overrun by locusts.

This history of the last outbreak has been reconstructed from the information collected mainly by inquiries from local officials and can be only approximately correct. The data left no doubt as to the Takmak-Kula area being a probable reservation, but it did not appear to me reasonable to suggest that this is the only reservation in the whole of Western Anatolia.

Search for other reservations was based on the idea that those areas where locusts breed in considerable numbers during the period of minimum should be considered at least as probable sources of outbreaks. I therefore decided to visit as many as possible of the localities where locusts were reported to have appeared at least in small concentrations during the last two or three years. Since my time was short, it proved impossible to complete the programme, but all the most important districts were visited and the ecological conditions of the breeding areas studied so far as the season permitted.

As a result, the following list of reservations of the Moroccan locust in Western Anatolia has been made (see map) :—

1. Environs of Kula, in the direction of Takmak.
2. Environs of Gördis (not visited).
3. South-west of Demirchi.
4. Chivril (not visited).
5. Buladan (not visited).
6. Chibukly-Dagh, opposite Ortakche.
7. Mashat, in the mountains S.W. of Tireh.
8. Emiralem, between Menemen and Manisa.

Although this list is admittedly incomplete and several other reservation areas will be probably revealed by more exhaustive investigations, it should comprise all the main areas, and from this point of view it has a definite practical value in evolving a policy of preventive control. This practical side of the problem, however, is mainly of local interest only and has been dealt with at some length in my official report to the Turkish Government. Here it would be more interesting to give a general survey of the conditions common to reservation areas, since the conclusions reached may be helpful for other entomologists.

Physiography of Reservations.

The main features of the structure of Western Anatolia are as follows : The great inner plateau of Asia Minor is limited in the west by a series of mountain ranges, running roughly in a semicircle. To the west of these ranges the country slopes somewhat rapidly towards the Mediterranean Sea, but this generally sloping country is intersected by a series of large river valleys which have a more or less east-west direction. The main rivers in the southern half of Western Anatolia, which half alone interests us at present, are Gedis-chai, Kuchuk-Menderes and Biyuk-Menderes, and their three valleys are separated from each other by moderately high mountain ridges arising from the margin of the plateau and running from east to west.

A glance at the map is sufficient to show that all the reservations have a definite relation to the physico-geographical features of the country. To begin with, there are no reservations on the plateau itself, and none in the valleys, but they are to be found either on the slopes of the plateau or of the mountain ridges separating

river valleys. In all cases, without exception, they are within the same altitudinal zone, namely between 500 and 1,000 metres above sea-level. It would be possible, perhaps, to define the normal altitude of reservation areas even more exactly by taking barometer readings at the actual places; judging from the known altitudes of the nearest villages, or other geographical points, most reservations are at an altitude of about 800 metres.

Altitude above sea-level cannot in itself constitute a condition favourable or unfavourable for locust breeding, and we must turn our attention to the study of other conditions of reservations.

Vegetation in Reservations.

The natural vegetation of reservations represents a feature relatively easy to study, and it can be correctly considered as a true index to a number of other factors more difficult to observe, such as soils and climate.

There are many vegetational features characterising the area within which the locust reservations are to be found. As we move from the fertile valleys of Western Anatolia into the mountains, we soon reach the zone where the olive tree, a typical feature of the landscape of Mediterranean plains and foot-hills, begins to disappear. If we compare the upper limit of olive cultivation with the position of reservations (see map), we shall see that the latter can be found only considerably higher up than the former. In other words, reservations are possible only well beyond the limits within which the cultivation of olives is practicable.

Another very interesting and significant comparison can be made between the altitudinal limits of the Valonia oak (*Quercus aegilops*) and the location of reservations. It will be seen from the map that all the most important reservations are situated very close to the upper limit of the distribution of this oak. Particularly striking is this condition in the Demirchi area, where the reservations are actually found between the widely scattered trees of this oak. Similar conditions were observed in the Chibukly-Dagh reservations, and it is interesting to note that the mean altitudinal limit of *Quercus aegilops* in Anatolia has been determined at 867 metres (Koch, 1910), a figure strikingly near that for reservations.

Still more important and significant appears the relation between reservations and the lower (or western) boundary of the extensive grass steppes which cover the greater part of the inner plateau. The exact limits of the steppes are not known, but investigations by Philippson (1919) made the approximate boundary sufficiently clear, and I have been able to introduce some corrections to it on the basis of my observations in the Demirchi area. This corrected boundary is shown on the map by a line of black dots, and it will be noticed that most reservations are found close to, and immediately under, this boundary. In other words, the Moroccan locust finds the conditions suitable for the formation of the swarming phase in the immediate vicinity of the steppe region, but not in that region itself. This conclusion is undoubtedly of great practical importance, since it permits us to state that locust reservations should be looked for in a relatively narrow zone bordering the steppes from below.

These general botanico-geographical features of the reservation zone may appear less definite on the map than as described above. For instance, it may be argued that the reservations in the Menemen district, or those in the mountains south of Tireh, are situated very far from steppes, and appear to have no relation to the boundaries of the distribution of olive trees or of the Valonia oak. However, it must be realised that the botanical boundaries shown on the map refer only to the major areas of continuous distribution of the respective plants, and do not represent their vertical distribution on the isolated mountain ranges. My actual observations in the Menemen district showed that the reservations there are again well

above the upper limit of olive cultivation and also near the limit of the Valonia oak. Similar conditions obtain in the Mashat reservation, south of Tireh. In both these areas the mountains are, however, not sufficiently high for the steppe vegetation to appear, and therefore the third condition typical for a main reservation area is naturally not fulfilled.

While we have thus outlined a fairly definite zone within which reservations are known to occur, this does not mean that the whole of that zone represents a potential breeding-ground for the swarming phase of the locust. Indeed, my studies on the ecology of several areas where eggs have actually been laid this year showed that the requirements of the locust when laying eggs are extremely narrow, and consequently the eggs are always concentrated in relatively small isolated spots, often only a few square metres in extent. This was particularly strikingly demonstrated in Demirchi and Kula reservations.

The Demirchi reservation area occupies the slopes on the right side of the valley of the Demirchi River, from Chatmuli for about 15 km. along the main road to Borlu. A sketch-map of the egg-deposits during 1930 and 1931, prepared by Haidar Bey, the agricultural officer in Demirchi, illustrates very clearly how little the position of the deposits is changed from year to year. The whole area is about 2–4 km. wide, but it would be incorrect to assume that even this restricted area is infested throughout. The slopes of the valley are dissected by numerous small secondary valleys and ravines running towards the river, and the distribution of plants is greatly affected by these details of the relief. The whole area, if regarded from a distance, *e.g.* from the opposite slope of the main valley, presents a very peculiar aspect of greyish, apparently bare, slopes dotted with regularly shaped round grey-green trees of Valonia oak.

On a closer examination of the vegetation of the slopes, it will be found that the oaks are distributed unevenly and form somewhat denser stands in depressions, or on the slopes of secondary valleys. Crests of the small ridges separating these valleys from each other are, on the contrary, characterised by the trees standing very wide apart, or even absent altogether, and by very scanty other vegetation, which is quite characteristic in its composition. The actual spots where the eggs are found are usually the barest of all, often with large outcropping stones, and only the following few species of plants* have been found on them :—

Plantago sp. aff. *bellardi*	*Gypsophila venusta*
Trifolium lagopus	*Heliotropium europaeum*
Hordeum crinitum	*Eryngium creticum*
Cynodon dactylon	*Allium paniculatum*

Most of these plants were represented by isolated individuals, and only two deserve our special attention. One is the *Plantago*, a minute ephemeral species, which was in July represented by completely dried up stems about two inches high, with a narrow hairy head, more resembling a small graminaceous plant than an ordinary *Plantago*. It grows on otherwise almost bare spots and forms a fairly dense cover ; when looking against the sun the plants appear silvery-grey and the spots covered by them stand out very distinctly from the surrounding yellowish areas in which *Hordeum crinitum* predominates. It is clear that this *Plantago* is restricted to the driest and most open soils in the vicinity of stone outcrops, and since the locust eggs are also concentrated in such spots, one must conclude that the requirements of the plant and the ovipositing locust as regards the composition of the soil and the microclimate are identical. It appears possible, therefore, to find actual egg deposits by the presence of the plant, and indeed digging in the spots covered by the *Plantago* almost invariably revealed the presence of eggs, while no eggs could be found in the areas covered by *Hordeum* only 2–3 feet away.

* I am greatly obliged to Dr. H. Krause, Biologisches Reichsanstalt, Berlin, for the identification of my plants.

Another plant of interest proved to be a grass, *Cynodon dactylon*, called *ayrik* in Turkish, which grows also on the barest spots, where it spreads its creeping branched stems. The importance of *ayrik* was demonstrated particularly well in Kula reservations. These are situated on the right side of the small river Sogut-chai, on a sloping plateau, intersected by numerous small secondary valleys. The slopes are generally bare of trees, except some scattered bushes of *Paliurus aculeatus*, and the general vegetation is otherwise composed of the same plants as in Demirchi area. Egg-deposits were invariably found on the more prominent points, often marked with outcrops of stones, of the ridges separating secondary valleys. The dominant, or at any rate the most conspicuous, plant of these places was again the same silvery-grey dwarf *Plantago*. Bare spots, inadequately covered with this plant, often bore colonies of *ayrik*, and locust eggs, while present throughout the spot, were found to be more concentrated between the roots of the *ayrik*.

It is obvious that the ecological rôle of these two plants in relation to the locust is not the same. *Plantago* simply denotes the spots most preferred by female locusts for oviposition, while *Cynodon dactylon* serves to concentrate the egg-laying locusts round itself. This concentrating rôle of *Cynodon dactylon* has been recently observed also in Turkestan with regard to eggs of *Calliptamus* (Lepeshkin, Zimin & Spassky, 1931), but the actual mechanism of this concentration remains obscure. It might be assumed that *Cynodon* attracts females as food, other plants being at that time dried up, but with *Calliptamus* this is certainly not the case, because that species of locust prefers feeding on non-graminaceous plants. The Russian authors are inclined to think that the attraction of *Cynodon* consists in the shade the plant provides for ovipositing females and in the physical conditions of the soil between the roots of the plant. In the case of the Moroccan locust, *Cynodon* would probably be a very acceptable food, but direct observations on egg-laying are necessary before the reason for the attraction can be found.

In any case, my observations have revealed some very important points in the ecology of the Moroccan locust in reservations. First of all, from the practical point of view it is obviously important to know that the actual egg-laying places are very restricted and that the suitable spots can be recognised by the presence of certain plants. Further, this restriction of egg-laying sites and the concentration of eggs near clumps of *Cynodon* may be a factor of outstanding importance in the formation of the swarming phase. To this aspect of the problem we shall, however, return later (see p. 286).

Influence of Climate.

While the vegetation, as we have just seen, supplies some very useful indications with regard to locust reservations, it is clear that its influence is mainly indirect. The facts pointed out above suggest mainly that there is a significant coincidence in the requirements of the locust and of certain plants with regard to other factors, of which soil and climate are the most important. Unfortunately, I was unable to undertake a study of the soils and this is a problem for future investigators, but as regards climate, the data at hand, although less complete and reliable than might be desired, are sufficiently helpful for understanding the problem of locust reservations.

As is well known, several climatic regions can be distinguished in Asia Minor (Zistler, 1926), but of these only two are of direct interest to our problem, namely, the steppe region and the Mediterranean, or more exactly, the Aegean region. Their climates differ strongly in temperature regime, and still more in precipitation. The annual amount of precipitation in the Aegean region, which comprises the plains and lower hills of Western Anatolia, varies according to locality and year from 500 to 1,000 mm., most of it falling in the winter months ; while in the steppe region the annual precipitation is 200–500 mm. and the maximum falls in spring (about May).

The zone within which locust reservations are found does not belong properly to any of these two climatic regions, but is situated almost exactly on their boundary. The precipitation regime of the zone is, therefore, an intermediate one. This is strikingly demonstrated by Table I and fig. 3, which illustrate the monthly distribution of precipitation on the inner plateau itself (average figures for Ankara and

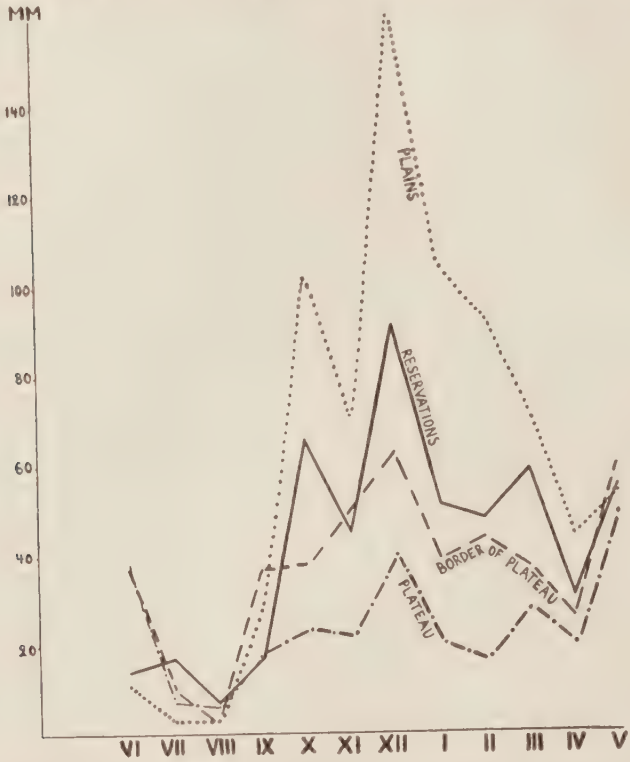


Fig. 3. Graphs of mean monthly precipitation in the main climatic zones of Western Anatolia.

Konya), on the western margin of the plateau (Afyon-Karahissar, Ushak), in the reservation zone (Kula and Demirchi), and in the plains (Manisa, Aydin and Ödemish).* It will be noticed that the table and the graphs begin with June and end with May; this arrangement is in agreement with the annual cycle of the locust, which lays its eggs about June, hoppers hatch in March–April, and adults reach maturity in May. It is obviously more correct to study the precipitation with reference to the life-history, particularly when it is not the average figures for several years that are analysed, but the actual ones for definite years.

The table shows that the annual total of precipitation falling on the plateau is very small, from 250 mm. in the interior, to 446 mm. on the border, while on the plains an average figure of 775 mm. is attained and over 1,000 mm. is registered in individual years. The zone of reservations scarcely differs in this respect from the western border of the plateau.

Still greater, and probably more significant, differences between the regions studied can be observed in the monthly and seasonal distribution of precipitation. On the plains, a very high maximum of precipitation is observed in December, while on the plateau there is a maximum in May, with a rather low second maximum

* I am greatly obliged to Ahmet Tevfik Bey, Director of the Meteorological Institute, Ankara, for supplying me with the meteorological data.

in December. On the border of the plateau, the December maximum becomes slightly higher than the May one, and in the reservation zone, the general monthly distribution of precipitation is of the plains type; though the amounts falling in individual months, and in whole years, are consistently lower and the differences

TABLE I.

Monthly means of precipitation in different areas (figures represent the averages for 2–3 stations in each area for the years 1927–1930, taken from Tevfik, 1931).

	VI	VII	VIII	IX	X	XI	XII	I	II	III	IV	V	Total
Inner plateau	28	7	6	18	23	22	40	21	17	28	20	50	270
Border of plateau	37	10	3	37	38	47	73	39	44	37	26	60	446
Reservations	14	17	7	17	65	45	91	51	48	59	31	55	488
Plains	11	3	3	29	102	71	161	106	94	72	44	54	755

between months less pronounced. Speaking generally, the monthly distribution of precipitation in the reservation zone is more regular than on the plains.

It is of interest from our point of view to compare the seasonal distribution of precipitation in different areas. This is illustrated by fig. 4. The graph shows

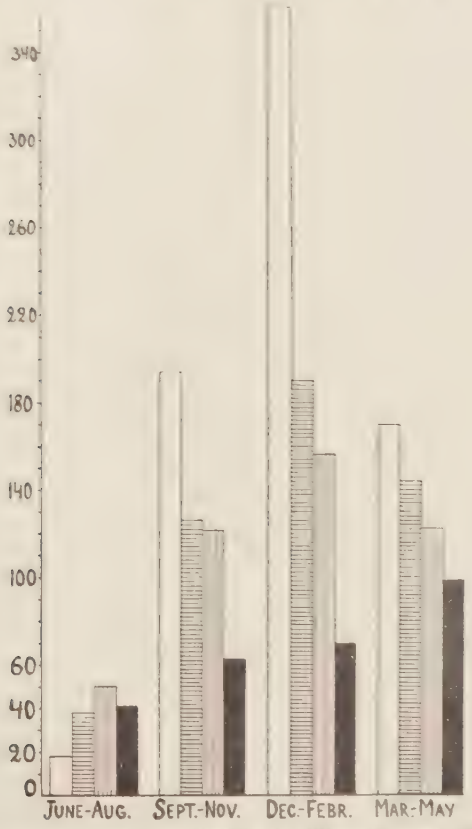


Fig. 4. Seasonal distribution of precipitation in different zones. White=plains; horizontal rulings=reservations; vertical rulings=border of the plateau; black=central plateau.

very strikingly the tremendous seasonal variation observed on the plains and the relatively more equable regime of the plateau, where, however, the absolute amount of precipitation falling in any season, except summer, is much lower than elsewhere. The difference in this respect between the reservation zone and the border of the plateau is very small.

The temperature regime of the respective regions is also very different. The inner plateau is characterised by a severe winter, with frosts, while on the plains the winter is extremely mild and the temperature only very seldom falls below freezing point, the average mean temperature of February, which is the coldest month, being between 5° and 10° C. It will be more convenient, however, to study the temperature relations in connection with precipitation and the life-history of the locusts, and this will be done in the next section.

Factors limiting the Moroccan Locust.

The first essential requisite for analysing the probable cause of outbreaks of any insect pest is a knowledge of its principal physiological characters, such as the vital limits of temperature and humidity in all stages, the velocity of development under various conditions, the influence of environmental factors on fertility, etc. It is needless to say that the Moroccan locust has been just as little studied in this respect as most other pests, and a few data of this character communicated by La Baume (Bücher, 1918) are much too vague and general to be of immediate value in epidemiological work.

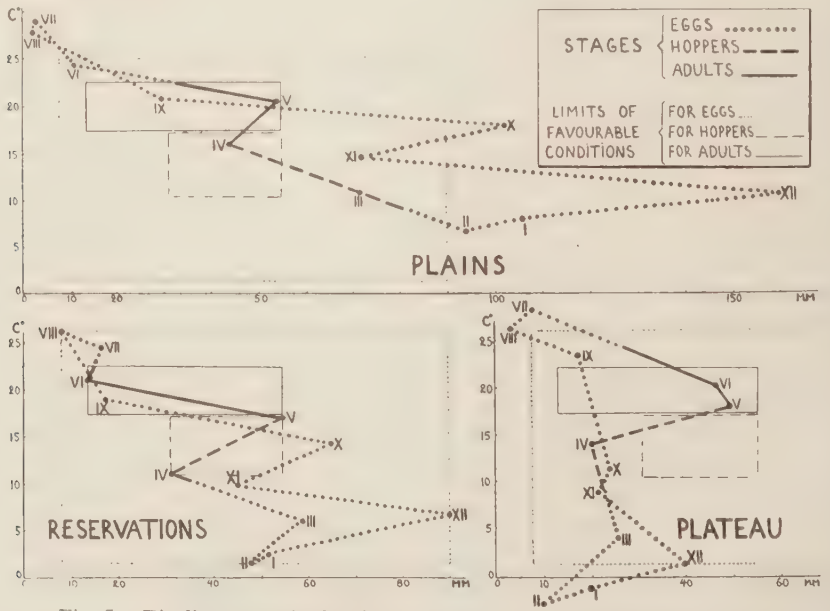


Fig. 5. Bioclimatographs for three main zones. For discussion see text.

In the circumstances we are forced, therefore, to adopt the less satisfactory indirect method of studying the environmental influences which may lead to outbreaks. This consists in a comparative analysis of environmental conditions in different areas and in different years by means of the climatograph method.

The climatograph method in general has been recently discussed by me (Uvarov, 1931), but here I venture to offer a new modification of it which appears to make easier the comparison of climates in relation to the life-history of the insect. A more complete discussion of the new method will be given elsewhere, but the present case offers the first attempt to use it in practice.

The idea of the *bioclimatograph* is a variation of the usual Ball–Taylor climatograph, in which each month of the year is characterised by the mean monthly temperature (on the vertical ordinate) and the total precipitation for the month (on the horizontal ordinate); the points for respective months are then joined by a line in the order of months. The variation consists in representing the seasonal life-history of the insect under study on the same graph. This is done by utilising the line connecting monthly points to represent the stages in which the insect passes the respective months. A glance at fig. 5 will make the idea clear.

The bioclimatographs (fig. 5) for the Moroccan locust in three main areas under study must be regarded as only preliminary ones, since both the meteorological data for the respective areas, and still more the life-history of the locust in each area, are very insufficiently known. Indeed, it must be pointed out that the temperature data for the reservation zone are not even the actual ones based on observations. It is an unfortunate fact that there is not a single station recording temperatures in the whole area of reservations, and it was possible to draw the climatograph only by calculating the temperatures for respective months, by interpolation, from the temperatures of the stations situated at higher and lower altitudes. This inexactitude of existing data prevented the possibility of including in our analysis the zone of the plateau border, since it would have been difficult to differentiate between the accidental and the significant variation in the data.

A study of the bioclimatographs permits the following general deductions to be drawn.

The longest stage in the development of the Moroccan locust is the egg. Eggs are laid in the early summer and have a very long diapause, hatching only next spring. They are, therefore, exposed to a very wide range of conditions. In the reservation zone, eggs are exposed to very high temperatures and very low humidity during the second half of the summer, and a diapause due to lack of moisture is the result. Good rains begin only in October, when the temperatures are presumably too low for continuous development of the embryo, and the diapause, which was induced at first by the deficient humidity, is continued owing to the deficiency in heat. Incubation can be resumed only in April, when both the temperatures and soil humidity are favourable.

The range of conditions to which eggs are subjected in reservations can be graphically expressed by drawing vertical lines to represent the maximum and minimum precipitation (in December and August respectively) and two horizontal lines for the maximum and minimum limits of temperature (in August and February); these four lines form a *quadrangle of favourable conditions* for eggs. If we now superimpose this quadrangle on the bioclimatograph for the plains, we shall see at once what particular climatic features of the plains can be suspected to be unfavourable to locust eggs. It will be seen (fig. 5, plains) that the egg curve lies within the favourable quadrangle on a very considerable portion of its length, but projects beyond its limits at the two opposite ends. The fact that locust eggs in the plains are exposed to a somewhat higher temperature and lower humidity during July-August than is the case in reservations, is scarcely of any significance, since the dormant eggs should be able to withstand these conditions without any injury. Far more interesting is the fact that the winter portion of the climatograph for the plains lies almost wholly outside the favourable quadrangle. Copious rainfall during October, November and December, is coupled there with temperatures sufficiently high to break the diapause, and cases of eggs hatching in late autumn and even in winter should be possible. Indeed, preliminary experiments by Plotnikov (1912) demonstrated that eggs of the Moroccan locust can be forced to develop without a diapause, if kept at a favourable temperature and high humidity. It stands to reason that hoppers appearing in autumn, or in winter have a very small chance of surviving until the adult stage. Moreover, a moist and warm winter should be

favourable to the development of fungous diseases in eggs, but this is a theoretical consideration which should be tested in future.

Let us compare now the conditions for larval development in the reservations and on the plains. Hatching occurs in the reservations, on the average, during the second half of April and the adult stage is reached by the end of May. On the plains, the main mass of hoppers would hatch about the end of March and would become adult by May. If we again draw a quadrangle of favourable conditions for hoppers in the reservations and superimpose it on the climatograph for the plains, we shall see that the development of the hoppers on the plains has to occur at a much higher humidity than in the reservations, while the temperature conditions are practically identical in two cases. This means that excessive moisture in spring may constitute another important factor controlling locust numbers on the plains.

As regards the adult locust, the section of the bioclimatograph for the plains referring to the adult stage falls within the favourable quadrangle, and there is no definite indication of any significant controlling conditions for this stage.

While, thus, our analysis permitted us to draw fairly definite conclusions with regard to the probable controlling factors on the plains, the application of the same bioclimatograph method to the conditions prevailing on the plateau, where locusts also are unable to breed in the swarming phase, gives less satisfactory results. Indeed, the conditions of the adult life on the plateau do not seem to differ at all from those in the reservation zone (fig. 5, plateau). In the hopper stage, the temperature conditions on the plateau are favourable throughout, while there appears to be some deficiency in the moisture during the first half of the hopper stage. It is highly doubtful, however, that this can be an effective controlling factor. Conditions for eggs in summer and autumn are apparently quite favourable. In winter the precipitation is well below that in the reservations, but this factor in itself again can scarcely be admitted as a possible controlling influence, since the winter temperatures are in any case too low for embryonic development. The only deviation of the egg graph from favourable conditions is observed in its bottom portion, referring to the winter months. Here we see the temperatures very much lower than those to which the eggs are exposed in the reservations. At the same time, there is a very low amount of precipitation, which in this case means a thin snow cover insufficient to protect the eggs from frosts. This suggests that the factor controlling locusts on the plateau consists in winter frosts, but this conclusion has to be carefully checked by field observations and by exact experiments.

In order to obtain a clear idea as to the factors which make the reservations particularly favourable for the development of the swarming phase, it would be necessary to compare their conditions not only with the extreme cases of the plateau and plains, but also with the neighbouring regions. Particularly interesting should be a comparison between the reservation zone and the border of the plateau, but all my attempts in this direction proved to be fruitless, because of the lack of sufficiently reliable meteorological data for both areas. Therefore, a more exact definition of favourable conditions must be left to future investigators.

The Course of Outbreaks.

Although the conditions in the reservations must be generally favourable for the existence of locusts, they should include some controlling elements as well, because otherwise the locusts would have been always very numerous in them, and this is not the case. Actually, the locusts are always present there only in moderate numbers and in the solitary phase, and only in certain periods do their numbers begin to increase and the swarming phase make its appearance. In studying the epidemiology of any swarming locust these two features, *viz.*, the increase in numbers and the transformation into the swarming phase must be analysed separately.

We have seen above that the amount of winter precipitation represents one of the most important controlling factors for the Moroccan locust. It is very significant, therefore, that the zone of reservations presents a peculiarity in this respect as compared with the plateau and plains. The curves (fig. 6) representing the monthly

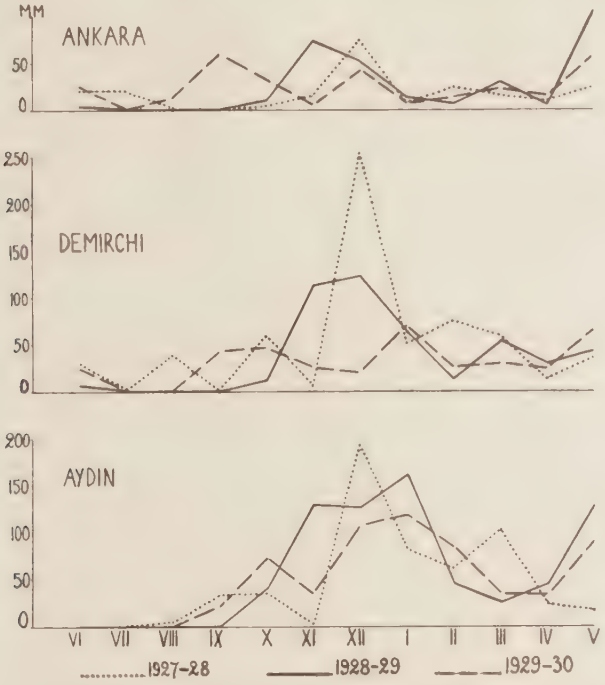


Fig. 6. Curves of monthly precipitation for three successive years on the plains (Aydin), in the reservations (Demirchi) and on the plateau (Ankara).

amounts of precipitation during three successive years proved to retain practically the same shape in the case of a typical plateau station, Ankara, and a typical plains station, Aydin; but the curve for Demirchi, one of the reservation areas, showed extremely sharp fluctuations, particularly in regard to the amount of precipitation in the winter months. This is demonstrated also by the striking annual variations in the course of the isohyet separating the areas with 350–500 mm. annual precipitation from those with 500–650 mm., as shown on the map by solid black lines. This means that reservations are characterised by a very unstable precipitation regime, particularly in winter. These yearly fluctuations of the most critical factor cannot fail to exert their influence on the locust numbers in the reservations, and these numbers should be expected to fluctuate accordingly. The conditions of the plateau and plains are more constant, *i.e.*, they are always equally unfavourable to locusts. The fact that the Moroccan locust can survive in both these relatively unfavourable areas, though only in the solitary phase, indicates that the conditions are inimical not to its survival, but to an increase in its numbers. The number of locusts in a given area can remain the same on the condition that each pair produces only a pair of progeny. The reproductive powers of the Moroccan locust are not known exactly, but for argument's sake it can be assumed that a female produces on the average three egg-masses, or about 100 eggs. Out of this number, only two individuals should survive, if the numbers are not to increase. Thus, not less than

98% of the progeny must be normally eliminated in those areas where no strong fluctuations in locust numbers are observed. This is, then, what happens regularly on the plains and on the plateau, while in the reservation zone, where the critical factor (winter precipitation) is very unstable, the percentage of survival should be expected to fluctuate from year to year and the locust population cannot remain constant. Thus, we arrive at a very interesting conclusion, that the instability of the critical factor (of course within certain limits) constitutes an important, probably even the decisive, character of the reservations. This conclusion appears to be applicable to other swarming locusts as well, though the actual critical factor may be very different in each case, but it would be out of place to discuss the general epidemiology of locusts here.

A mere increase in numbers of solitary locusts does not yet constitute the beginning of swarming, and a study of the conditions leading to the production of the swarming phase is an obvious necessity. From what we know with regard to locust phases in general, there is no reason to think that the swarming phase can be produced from the solitary by the influence of any environmental conditions, except by crowding of a large number of hoppers in a restricted area. Although the phases of the Moroccan locust have not yet been studied experimentally, there is no valid reason to suppose that this species will prove to be an exception, and we can assume that its swarming phase is also a result of crowding.

Regarded from this point of view, the extremely narrow and strictly defined egg-laying sites within reservations (see p. 278) assume a great epidemiological significance. Indeed, any considerable increase in the percentage of locust eggs surviving a particular winter would mean a corresponding increase in the actual density of the population within the relatively small hatching areas, and a transformation into the swarming phase must inevitably follow. Again, the tendency of female locusts to lay eggs, for example, in clumps of *Cynodon dactylon* is another concentrating factor which cannot fail to favour the development of the swarming phase in the next generation. Further, the fluctuations in the precipitation which are typical for the reservation zone cannot remain without an influence on the size of the egg-laying spots. These spots, as we have seen, are restricted mainly to the barest hillocks, with typical vegetation. It stands to reason that in a very dry year the size of the bare spots would have a tendency to increase, while in wet years a less xerophilous vegetation (*Hordeum*, etc.) would tend to invade the hillocks, thus reducing their areas. In this way, the density of the locust population would be affected both by the actual increase or decrease in the locust numbers, and by the expansion or contraction of the individual breeding spots.

Of course, these are mainly theoretical considerations, which remain to be checked by future investigations, but they have at least the advantage of demonstrating how exceedingly complicated can be the conditions leading to locust outbreaks in reservations.

These considerations might be brought nearer to the actual state of things, if we had at our disposal a sufficiently long and continuous series of meteorological data for the reservation zone, comprising a period of the beginning of an outbreak. Unfortunately no such data are available, and we are unable even to find any indication as to the direction in which the critical factors should deviate from the mean conditions in order to start an outbreak. In order to obtain such data it would be necessary to establish a meteorological station within the reservation zone, where there are none at present.

The formation of the swarming phase in the reservations is followed by the swarms spreading into adjoining territories (see fig. 2). The question now arises, how the existence of swarms proves to be possible outside the reservation zone, *i.e.*, under conditions which are admittedly unfavourable for this phase?

We know that the meteorological conditions in the invasion areas are not wholly unsuitable to the Moroccan locust, but merely do not permit an increase in its numbers, which are always maintained at the same level by a "normal" elimination of about 98% of the progeny. There is no reason to think that the factors controlling local locusts would have a different effect on the invading swarms. Therefore, when large masses of locusts invade these areas, the percentage of destruction amongst their progeny should remain the same, that is 98%, and this means that in the next generation the swarms will be just as numerous as the original invaders, and the invasion will continue. When, moreover, there is even a slight deviation in the general weather conditions in a favourable direction, the percentage of destruction becomes less than 98%, and a rapid increase in locust numbers follows. Fresh invading swarms emerging from reservations in the next season augment the locust numbers still more, and the invasion gradually spreads wider and wider, until swarms reach the zones entirely unsuitable for breeding, or until the general climatic conditions take a sharp turn in an unfavourable direction.

The history of the last great invasion, in 1909–1918, was in full accordance with this general scheme (see fig. 2). The outbreak began in the reservations between Kula and Takmak (probably in some others as well) and the swarms then spread gradually over the greater part of Western Anatolia, causing incalculable damage. There is no reason to think that the next outbreak will follow a different course, and the knowledge of locust reservations and of their ecological conditions must form a basis for planning rational control measures aiming at the *prevention* of the outbreak. These measures should include a complete survey of the possible reservation areas, investigations on their ecology and especially the climate, and a carefully considered scheme for keeping all reservations under observation and for controlling all incipient congregations of locusts.

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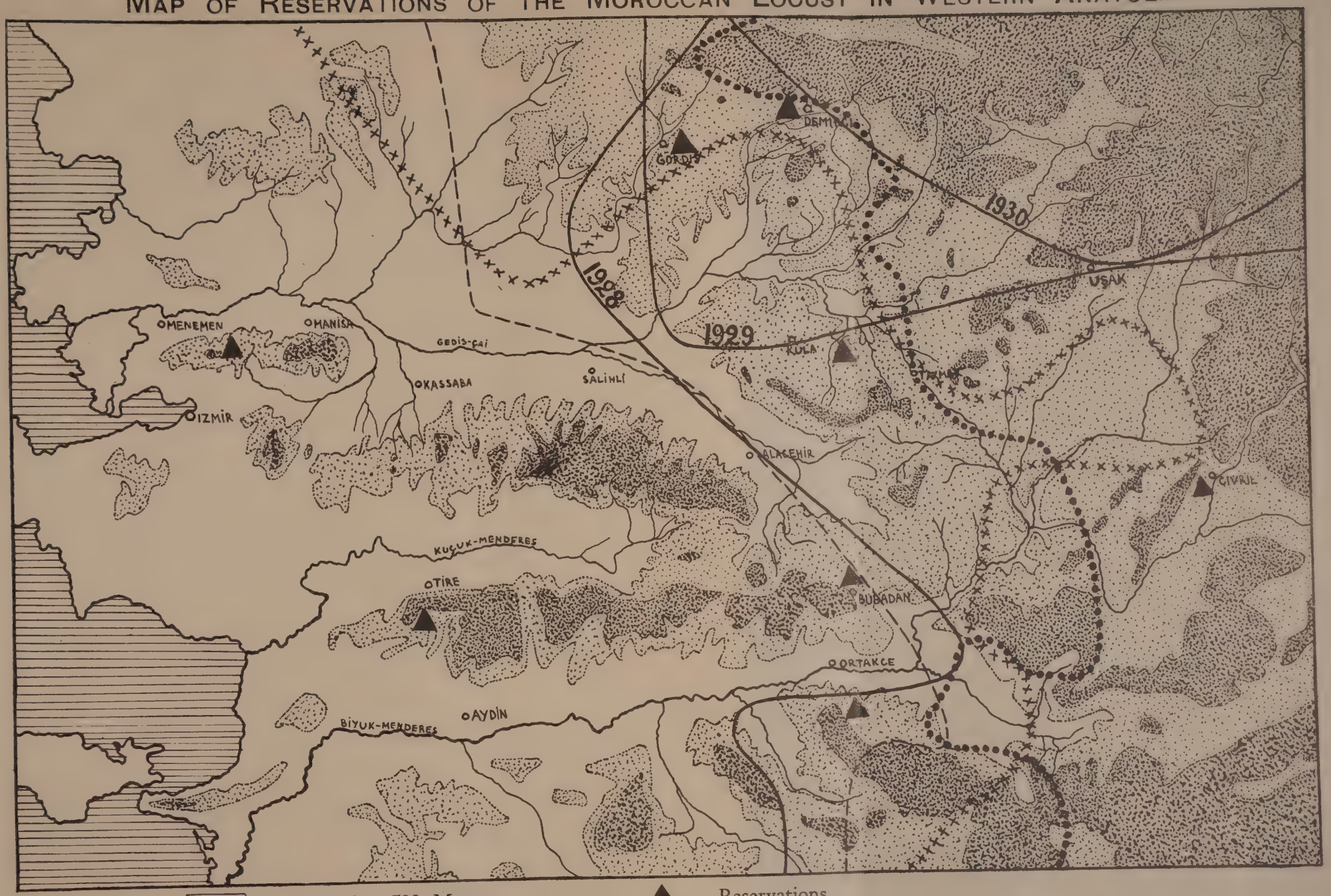
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Map of Reservations of the Moroccan Locust in Western Anatolia



= Sea Level— 500 Metres.
= 500—1,000 „
= over 1,000 „

▲ = Reservations.
– – – – = Eastern (and upper) limit of Olive Cultivation.
X X X X = „ „ „ „ „ Valonia Oak.
●●●●●● = Western (and lower) „ „ Steppe.

——— = Isohyets for respective years, separating areas with the annual precipitation of 350—500 mm. (to the east and north of the line) and of 500—650 mm. (to the west and south of the line).

(Vegetation data after Philippson, with modifications; meteorological data after Tevfik.)

COLLECTIONS RECEIVED.

The following collections were received by the Imperial Institute of Entomology between 1st January and 31st March, 1932, and the thanks of the Managing Committee are tendered to the contributors for their kind assistance :—

Messrs. Stafford Allen & Sons, Ltd. : 70 Coleoptera and 70 early stages ; from England.

Mr. A. M. Altson :—25 Diptera and 6 pupa-cases, 13 Parasitic Hymenoptera, and 2 Isoptera ; from Northern Rhodesia.

Mr. J. Balfour-Browne :—6 Culicidae, 334 other Diptera, 475 Coleoptera, 5 Parasitic Hymenoptera, and 13 Rhynchota ; from the Azores and Madeira.

Dr. H. F. Barnes :—10 Parasitic Hymenoptera ; from the United States of America.

Mr. A. H. Bastin :—2 Cecidomyiidae and 6 pupae ; from England.

Squadron-Leader E. B. C. Betts :—21 Orthoptera and 3 Scorpions ; from Arabia.

Dr. H. Blunck :—200 Parasitic Hymenoptera ; from Germany.

Dr. F. S. Bodenheimer :—2,430 Coleoptera and 10 larvae, 3 Parasitic Hymenoptera, 3 Formicidae, 10 Thysanoptera, 6 Rhynchota, 180 Orthoptera, 10 Dermaptera, and 12 Collembola ; from Palestine.

Dr. G. Bondar :—20 Coleoptera ; from Brazil.

Mr. P. Bovey :—46 Parasitic Hymenoptera ; from Switzerland.

Mr. H. Britten, Manchester Museum : 261 Parasitic Hymenoptera and 140 cocoons ; from England.

Dr. P. A. Buxton, London School of Tropical Medicine :—27 Tabanidae, 18 other Diptera, 4 Coleoptera, and 6 Rhynchota ; from various localities.

Mr. H. F. Carter, Medical Entomologist :—5 Scolytidae ; from Ceylon.

Chief Entomologist, Pretoria :—65 Parasitic Hymenoptera ; from South Africa.

Mr. G. H. Corbett, Government Entomologist :—91 Diptera, 55 Coleoptera, 30 Parasitic Hymenoptera, 49 other Hymenoptera, 43 Lepidoptera, 80 Isoptera, 21 Thysanoptera, 8 species of Coccidae, 1 species of Aphidae, 26 other Rhynchota, 3 Orthoptera, 30 Collembola, 200 Mites, and 2 Spiders ; from Malaya.

Dr. E. D. Dallas :—17 Lepidoptera ; from the Argentine.

Dr. A. Dampf :—4 Coleoptera ; from Mexico.

Dr. W. M. Davies :—6 Parasitic Hymenoptera ; from North Wales.

Entomologist, Bangalore :—2 Diptera, 7 Coleoptera, 1 species of Coccidae, 130 other Rhynchota, and a number of Mites ; from Mysore, India.

Miss M. G. Evans :—64 Parasitic Hymenoptera ; from England.

Mr. J. L. Froggatt :—7 Lepidoptera ; from New Guinea.

Mr. S. Garthside :—15 Cecidomyiidae and 26 Parasitic Hymenoptera ; from England.

Mr. G. C. Ghosh :—3 Curculionidae ; from Burma.

Mr. F. D. Golding, Government Entomologist :—5 Siphonaptera, 3 Diptera, 30 Coleoptera, 2 Cimicidae, 5 other Rhynchota, 117 Orthoptera and 500 early stages ; from Nigeria.

Government Entomologist, Coimbatore : —111 Parasitic Hymenoptera ; from South India.

Government Entomologist, Jerusalem :—21 Coleoptera, 9 Hymenoptera, 47 Lepidoptera, 2 Rhynchota, 12 Orthoptera, 20 Planipennia, 144 Odonata, and 2 Ephemeridae ; from Palestine.

Government Entomologist, Lyallpur :—4 Coleoptera, 37 Parasitic Hymenoptera, 4 other Hymenoptera, 42 Lepidoptera, 38 Rhynchota, 4 Orthoptera, 3 Planipennia, and 4 Odonata ; from the Punjab, India.

Mr. W. B. Gurney :—7 Coleoptera and 4 larvae, and 2 Thysanoptera ; from New South Wales.

Mr. F. C. Hadden :—253 Coleoptera ; from the Philippine Islands.

Mr. G. L. R. Hancock, Assistant Entomologist :—39 Culicidae, and 117 early stages, 105 *Haematopota*, 97 other Diptera, 10 Coleoptera, 290 Parasitic Hymenoptera, 324 Lepidoptera and 5 early stages, 79 Orthoptera, 8 Dermaptera, 7 Trichoptera, 6 Mallophaga, and 20 Mites ; from Uganda.

Mr. G. H. Hardy :—6 Diptera and 3 puparia ; from Queensland.

Mr. E. Hargreaves, Government Entomologist :—5 Culicidae, 10 Tabanidae, 191 other Diptera, 247 Coleoptera, 800 Parasitic Hymenoptera, 272 other Hymenoptera, 234 Lepidoptera, 207 Thysanoptera, 20 species of Coccidae, 1 species of Aphidae, 336 other Rhynchota, 113 Orthoptera, 32 Dermaptera, 6 Planipennia, 3 Ephemeridae, 34 Trichoptera, and 80 Mites ; from Sierra Leone.

Dr. A. J. Hesse :—2 Curculionidae ; from South Africa.

Mr. W. E. H. Hodson :—23 Coleoptera ; from Japan.

Mr. G. V. Hudson :—4 Lepidoptera ; from New Zealand.

Mr. A. Hustache :—103 Curculionidae ; from Africa.

Dr. A. D. Imms :—4 Parasitic Hymenoptera ; from Germany.

Dr. L. G. E. Kalshoven :—19 Curculionidae ; from the Dutch East Indies.

Mr. C. B. R. King :—30 Parasitic Hymenoptera ; from Ceylon.

Mr. S. Kozlovsky :—22 Parasitic Hymenoptera ; from Morocco.

Dr. W. A. Lamborn, Medical Entomologist :—100 Tabanid larvae and 2 egg-masses, 70 Parasitic Hymenoptera, and 30 Fulgorid nymphs ; from Nyasaland.

Dr. S. Leefmans :—6 Curculionidae and 58 Parasitic Hymenoptera ; from the Dutch East Indies.

Dr. R. H. Le Pelley :—40 Parasitic Hymenoptera, 13 Lepidoptera and 2 pupa cases, and 45 Rhynchota ; from Kenya Colony.

Mr. R. A. Lever, Government Entomologist :—4 Culicidae, 30 other Diptera, 134 Coleoptera, and 32 larvae, 21 Parasitic Hymenoptera, 37 other Hymenoptera, 21 Lepidoptera and 5 pupa-cases, 100 Isoptera, 1 species of Coccidae, 38 other Rhynchota, 12 Orthoptera, 8 Planipennia, 2 Odonata, 10 Mallophaga, 20 Anoplura, and 2 Scorpions ; from the Solomon Islands.

Mr. A. Da Costa Lima :—15 Coleoptera ; from Brazil.

Mr. J. B. Loughnane :—1 species of Aphidae ; from Ireland.

Mr. T. L. McClelland :—15 Coleoptera and 16 Orthoptera ; from Kenya Colony.

Mr. J. W. McHardy, Medical Entomologist :—1 Culicid ; from Tanganyika Territory.

Mr. H. Maneval :—85 Parasitic Hymenoptera ; from France.

Prof. F. J. Meggitt :—100 Coleoptera ; from Burma.

Mr. C. Menozzi :—58 Parasitic Hymenoptera ; from Italy.

Dr. D. Miller, Cawthron Institute :—20 Coleoptera, 6 Rhynchota and 6 nymphs ; from New Zealand.

Mr. H. M. Morris, Government Entomologist :—21 Diptera, 176 Coleoptera, 14 Chalcididae, 12 Lepidoptera, and 8 tubes of Mites ; from Cyprus.

Mr. M. C. Mossop :—10 Siphonaptera, 84 Coleoptera, 2 species of Aleurodidae, and 6 other Rhynchota ; from Southern Rhodesia.

Mr. A. Moutia, Assistant Entomologist :—5 Diptera, 7 Coleoptera, 7 Parasitic Hymenoptera, 7 other Hymenoptera, and 5 Lepidoptera ; from Mauritius.

Musée du Congo Belge, Tervueren :—4 Parasitic Hymenoptera, 3 Lepidoptera, 5 Coccidae, and 7 other Rhynchota ; from the Belgian Congo.

Dr. T. A. M. Nash :—109 Diptera and 5 Coleopterous larvae ; from Tanganyika Territory.

Natal Museum, Pietermaritzburg :—25 Diptera and 20 early stages ; from South Africa.

Mr. & Mrs. J. Ogilvie & Miss A. Mackie :—2 Culicidae, 9 Tabanidae, 266 other Diptera, 208 Coleoptera, 10 Parasitic Hymenoptera, 397 other Hymenoptera, 3 Lepidoptera, 148 Rhynchota, 289 Orthoptera, 2 Dermaptera, 11 Planipennia, 25 Odonata, 2 Ephemeridae, and 2 Ticks ; from South Africa.

Mr. R. W. Paine :—4 Culicidae, 35 Parasitic Hymenoptera, 7 Lepidoptera, 5 species of Coccidae, 1 species of Aphidae, 2 other Rhynchota, and 10 Mites ; from Fiji.

Mr. H. M. Pendlebury, Selangor Museum :—303 Coleoptera ; from Malaya

Mr. R. Pussard :—2 Ichneumonidae ; from France.

Mr. E. Reitter :—149 Curculionidae ; from China and the Caucasus.

Dr. A. Reyne :—2 Orthoptera ; from the Dutch East Indies.

Mr. A. H. Ritchie, Government Entomologist :—60 Parasitic Hymenoptera and a number of pupa-cases ; from Tanganyika Territory.

Mr. E. Rivnay :—55 Curculionidae ; from Palestine.

Mr. J. L. Roberts, Medical Entomologist :—65 Rodents ; from Kenya Colony.

Mr. Nihat Schewket Bey :—12 Coleoptera ; from Turkey in Asia.

Dr. M. Schwartz :—3 Coleoptera ; from Asia Minor.

Mr. H. W. Simmonds, Government Entomologist :—6 Coleoptera ; from Fiji.

Mr. H. D. Smith :—23 Braconidae ; from France.

Mr. E. R. Speyer :—220 Diptera, 30 Coleoptera and 2 larvae, 4 Orthoptera, 5,000 Collembola, 40 Mites, and 2 Myriopoda ; from England.

Stockholm Museum :—703 Coleoptera ; from China and Mongolia.

Dr. H. H. Storey, Plant Pathologist :—2 species of Aphidae ; from Tanganyika Territory.

Dr. J. M. Swaine :—2 Tenthredinidae and 3 larvae, and 100 Mites; from Canada.

Systematic Entomologist, Dehra Dun :—1,452 Coleoptera, 163 Chalcididae, and 308 Rhynchota ; from the United Provinces, India.

Mr. E. L. Taylor :—5 Siphonaptera ; from England.

Dr. P. Tchorbadjiev :—15 Diptera, 143 Coleoptera, 42 Parasitic Hymenoptera, 13 other Hymenoptera, 30 species of Coccidae, 23 other Rhynchota, and 27 Orthoptera ; from Bulgaria.

Mr. R. W. E. Tucker :—12 Parasitic Hymenoptera ; from Barbados.

United States National Museum, Washington :—1,079 Braconidae ; from the Philippine Islands.

Dr. V. P. Varde :—6 Orthoptera ; from the Punjab, India.

Mr. R. Veitch, Chief Entomologist :—2 Diptera, 14 Parasitic Hymenoptera, 5 Lepidoptera and 11 early stages, 8 species of Coccidae, 2 species of Aleurodidae, 27 other Rhynchota, and 30 Mites ; from Queensland.

Wellcome Tropical Research Laboratories, Khartoum :—114 Culicidae, 209 other Diptera, 258 Coleoptera, and 114 Hymenoptera ; from the Sudan.

Dr. F. Zacher :—100 Parasitic Hymenoptera and 10 Lepidoptera ; from Germany.

THE PHASES OF LOCUSTS IN SOUTH AFRICA.*

By Jacobus C. Faure,

Professor of Entomology, University of Pretoria, Union of South Africa.

(Plates XIV–XXXVIII and a Map.)

Table of Contents

Page

INTRODUCTION—

The theory of phases 298
The species dealt with in this paper 300

LOCUSTANA PARDALINA (WALKER)

Transformation of *solitaria* into *gregaria* 301
The coloration of the hoppers as the standard of comparison ... 302
Table I.—Hoppers taken in the field : Treatment 302
Results 304
Conclusion 305
Table II.—Adults taken in the field 305
Conclusion 307
Table III.—*Solitaria* hoppers collected and crowded 307
Extreme *solitaria* hoppers 307
Hoppers from incipient swarms 309
Conclusion 309
The biometrical study of the adults as the standard of comparison ... 309
The method of measuring 309
Table IV.—Description of material 310
Discussion of data 312
Table V.—Description of material 313
Discussion of data 315
Summary of tables IV and V 315
Transformation of *gregaria* into *solitaria* 317
The coloration of the hoppers 317
The general appearance of the adults 319
Isolation, Semi-Isolation and Crowding 319
Factors which Influence the Coloration of the Phase *solitaria* 320
Field observations 320
Experiments with painted boxes 321
White 322
Black 323
Deep mouse grey 323

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(518) Wt. P2773B/3557 1100 9/32 S.E.R., Ltd. Gp. 253.

Page

Aniline yellow 323
Bay brown 323
Experiments with painted gauze cylinders 324
Table VI.—Summary of the experiments on colours which gave positive results 324
Experiments with colours on which the results were largely negative 325
The problem of the green hopper 327
Attempts to produce green on growing food 327
Short gauze cylinders 327
Tall gauze cylinders 328
Table VII.—Celluloid cylinders 328
The progeny of green and non-green parents 329
Other attempts to produce green 330
The fate of the green colour under altered conditions of environment 330
Wire gauze cylinders on boards 330
Green backgrounds 330
Boxes painted in various colours 331
A moist atmosphere 331
A dry atmosphere 331
Various other tests 332
General conclusions on the green colour 332
Is chlorophyll present in the tissues of the green locusts? ... 334
Several changes in coloration during the development of one hopper.—Table VIII 334

NOMADACRIS SEPTEMFASCIATA (SERVILLE) 335

The hoppers 336
Description of the hopper in the fifth instar, phase *gregaria* ... 336
The phase *solitaria* 337
Isolation on growing food 338
Other isolations 338
The adults 339

LOCUSTA MIGRATORIA MIGRATORIOIDES, REICHE AND FAIRMAIRE

Known distribution in South Africa 339
Transformation of *solitaria* into *gregaria* 340
Source and treatment of material 340
General notes on development and behaviour 341
Differences between phases 341
The coloration of the hopper as the standard of comparison.—Table IX 342
Winter and summer crowds 343
General conclusions 343
The biometrical study of the adults as the standard of comparison 343
Material and methods 343

Page

Table X.—Males 345
Table XI.—Females 347
Summary of Tables X and XI 347
TRANSFORMATION OF *GREGARIA* INTO *SOLITARIA* 348
The coloration of the hoppers 348
The morphological characters of the adults 349
The effects of crowding and isolation upon the progeny of individual pairs.—Tables XII and XIII 349
RESEMBLANCE TO THE COLOUR OF THE ENVIRONMENT 351
Experiments in painted cages 351
White 352
Black 352
Deep mouse grey 353
Aniline yellow and bay brown 353
Summary of the experiments on colours which gave positive results.—Table XIV 353
Experiments with colours on which the results were largely negative 353
Experiments with coloured glass 354
Blinded hoppers in painted boxes 355
THE PROBLEM OF THE GREEN HOPPER 356
Gauze cylinders over growing food 356
Celluloid cylinders over growing food.—Table XV 356
The progeny of green and non-green parents 357
A constant supply of green food in a moist atmosphere 358
The fate of the green under altered conditions 358
Wire gauze cylinders on boards 358
Green backgrounds 359
Cages painted in various colours 359
A moist atmosphere 360
A dry atmosphere 360
Food devoid of chlorophyll 360
Miscellaneous experiments 361
General conclusions on the green colour 361
SEVERAL CHANGES IN COLORATION DURING THE DEVELOPMENT OF ONE HOPPER.—Table XVI 362

THE CAUSES UNDERLYING THE DEVELOPMENT OF THE *GREGARIA* CHARACTERS

GENERAL CONSIDERATIONS AND THEORIES 364
The essential characteristics of life under crowded conditions ... 364
The theory of locustine production 365
A classification of the types of coloration in locust hoppers 366
The morphological differences in adults 367
EXPERIMENTS AND OBSERVATIONS 368
Hoppers in a crowd of another species 369

Page

Hoppers isolated in cages surrounded by crowds 369
Attempts to force isolated hoppers into activity 370
Small cages of celluloid 371
The jarring apparatus 372
Results obtained in the jarring apparatus.—Table XVII ... 373
The effect of temperature 375
Experiments in rearing at constant temperatures 376
Table XVIII.—*L. pardalina* 376
Table XIX.—*L. m. migratorioides* 377
Summer and winter crowds 377
Moisture as a factor affecting variation towards the phase *gregaria* 378
The influence of light 380
The effects of diets 380

THE HYPOTHESIS THAT MENDELIAN INHERITANCE IS THE CAUSE OF DIFFERENCES IN COLORATION 381
Table XXI.—Cross : *gregaria* × *gregaria* 382
Table XXII.—Cross : *solitaria* × *solitaria* 383
Table XXIII.—Cross : *gregaria* × *solitaria* 384
Table XXIV.—F_2 of cross : *gregaria* × *gregaria* 384
Summary and conclusions 385
Biometrical comparisons of the isolated and crowded progeny of individual pairs of *L. pardalina* 387

THE DISTRIBUTION AND BREEDING GROUNDS OF *L. PARDALINA* 387
The range of invasion 388
The grassveld as a breeding ground 389
The permanent habitat 390
Other Acrididae associated with *L. pardalina* 391
The areas of incipient swarming 391
Prospects for the future 392

THE EMBRYONIC DIAPAUSE OF *L. PARDALINA* 393
Incubation 5 to 37 months after oviposition.—Table XXVI ... 393
Incubation two months after oviposition 395
Incubation immediately after oviposition 395
The stage of development of the embryo during diapause 396
Hatching delayed in spite of favourable conditions.—Table XXVII 397
A supposed case of delayed hatching on a large scale in the field ... 398

AN ALBINO RACE FOUND IN *L. PARDALINA* 398
The effect of crowding on albinos 399
Albinos on growing grass 400
Albinos in painted boxes 400
Albinos crossed with non-albinos 400

SCHISTOCERCA GREGARIA (FORSKÅL) 401
Notes on development 401
The phase *gregaria* 402
OBSERVATIONS ON NON-MIGRATORY GRASSHOPPERS 402
The effect of crowding 402
Oedaleus nigrofasciatus (De Geer) 402
Acanthacris ruficornis (F.) 403
Resemblance to the colour of the environment 403
REFERENCES 404

Introduction.

This paper is based on observations made during the last four years at the University of Pretoria. Most of the work was done in the summer seasons of 1929–30 and 1930–31, and the investigations were supported by the Carnegie Corporation of New York, by means of a grant made available by the Research Grant Board of the Union of South Africa. The writer also wishes to acknowledge his indebtedness to the Carnegie Corporation and the Research Grant Board for providing funds towards the publication of the results.

The Department of Agriculture has materially assisted the work by the loan of cages and other equipment, the provision of motor transport for occasional field trips, and by sending living material from the field.

My friend and colleague, Professor Dr. A. J. T. Janse, undertook the laborious task of preparing the coloured drawings from freshly killed specimens. He accomplished this with painstaking care and great accuracy, and it is with pleasure that I express my sincere appreciation of his important contribution.

Dr. T. J. Naudé and Mr. S. J. S. Marais collected valuable material and gave me much assistance in other aspects of the work.

To Mr. B. P. Uvarov I am indebted for valuable advice and criticism. Dr. B. de Loor and Mr. M. N. S. Immelman helped me in many ways, and several other colleagues gave me various useful suggestions. For material and literature I express my thanks to Messrs. R. W. Jack, B. N. Zolotarevsky, H. B. Johnston, A. H. Ritchie, W. V. Harris and A. H. de Vries.

Finally, it is a pleasure to acknowledge the splendid cooperation of those who acted at various times as assistants, namely Messrs. F. A. Squire, L. D. Bosman, H. A. F. Lea, E. E. Schaefer, M. J. Oosthuizen, W. Powell, P. C. Neethling and Miss M. Field.

The Theory of Phases.

The theory of phases in migratory locusts was first proposed by Uvarov (1921) in order to explain the inter-relationships of the different forms of *Locusta migratoria*, L. (=*L. danica*, L.) and *Locustana pardalina* (Walk.). In his book on locusts and grasshoppers, published in 1928, he gives a further detailed account of the theory, discusses the objections advanced against it, shows that phases have been found to occur in *Schistocerca gregaria* (Forsk.), and refers to observations indicating that phases also occur in *Schistocerca paranensis* (Burm.) and *Dociostaurus maroccanus* (Thnb.).

The following brief summary of the essential features of the theory is included here in order to explain the sense in which various terms are used in the present paper.

The invasions of migratory locusts have always been characterized by irregular fluctuations rather than by a regular periodicity. Whereas the species were formerly regarded as being more or less monomorphic, the phase theory states that they are polymorphic, especially in hopper coloration and in such adult characters as the shape of the pronotum and the relative length of the wings. The forms occurring in dense swarms have an almost constant type of hopper coloration, characterized by a definite pattern of black combined with orange or yellow or both ; the adults have longer wings and usually a more constricted pronotum. The forms living singly, like isolated grasshoppers, have a great variety of colours as hoppers, but never the black and orange of the swarm form, and as adults they have relatively shorter wings and in some species a carinated pronotum. Forms found in small loose swarms show types of coloration and adult morphology that are intermediate between the swarm and solitary types.

The term *phase* has been applied to the forms of these polymorphic species : the phase *solitaria* is the form living in isolation ; phase *transiens* has been used for the transitional forms, and the type found in large swarms is called the phase *gregaria*. Some writers, especially Zolotarevsky (1929), recognize subdivisions of the phase *transiens* : for forms varying from *solitaria* towards *gregaria* they use the term *congregans*, and those varying in the opposite direction are called *dissocians*. To the writer this seems to complicate matters unnecessarily ; since he has been unable to find characters by which these subdivisions of the phase *transiens* may be recognized with certainty, these terms are not used in the present paper. In the present state of our knowledge, it seems better to confine ourselves to the three main phases—*solitaria*, *transiens*, *gregaria*—especially in view of the very wide interpretation to which the term *transiens* lends itself. One readily agrees that it would be an enormous practical advantage if a given collection of *transiens* material could be classified, on the basis of colour or structure or both, as *transiens congregans* or *transiens dissocians*, for this would enable the entomologist to predict whether or not swarming is to be expected. But it remains to be proved that this subdivision is possible.

In all the species in which both *solitaria* and *gregaria* hoppers are known, there is a great difference in the coloration of the two phases, but the morphological characters of the adults do not vary to the same degree in all species. Among those whose phases are known best, *L. migratoria*, L., exhibits the greatest degree of variation in adult characters because the phase *solitaria* has a carinated and convex pronotum, in strong contrast to the straight or concave pronotum of the phase *gregaria*.

The phase theory postulates that the species exhibits the characters of the phase *gregaria* when it forms large swarms, and that individuals living in isolation cannot retain these characters, but must acquire those of the phase *solitaria* ; this transformation is not magical and immediate, but may extend over one or more generations, and intermediate forms are common. The theory therefore insists not only on the specific identity of the phases but also on the actual transformation of one phase into the other. It explains the apparent disappearance of swarming forms by stating that the insects are still present, but are disguised as non-swarming grasshoppers which may even be known under other specific names.

Two features of Uvarov's account should be modified, in the opinion of the writer. On pages 148 and 160 of his book (1928), there are statements to the effect that the variation towards one phase or the other usually occurs simultaneously in all individuals of the species in a given locality. This might be interpreted to mean that the variation towards *gregaria* takes place regardless of the density of population, although it is clear from Uvarov's account that this is not his idea. To me there is no question whatever that the *gregaria* characters only begin to develop when and where density of population makes this possible.

The second point is the statement (page 153) that the hoppers of *danica* do not exhibit any tendency towards gregariousness. In cages, the *solitaria* hoppers of *L. pardalina* brought in from the field developed a good degree of activity when crowded together and soon began to show *gregaria* characters. In the field, loose aggregations of hoppers consisting of a mixture of *solitaria*, *transiens* and *gregaria* types are often encountered. I should therefore modify Uvarov's statement to the effect that the hoppers do not exhibit gregariousness until there are so many of them in a given locality that the individuals repeatedly come into sufficiently close contact with one another to awaken the tendency to gregariousness.

The theory of phases has been accepted by most entomologists working on locust problems, and most of the observations published since the theory was first proposed have tended to support it. The criticisms of Plotnikov (1927) and Potgieter (1929) will be briefly discussed.

The rather complicated and largely theoretical arguments advanced against the

theory by Plotnikov have been summarized and answered by Uvarov in his book. Plotnikov's theory amounts briefly to this: *danica* and *migratoria* are two independent races which can hybridise; under artificial conditions both races may also produce aberrations (due to crowding and isolation), which vary in the direction of the opposite form and differ from the hybrids only in their history. The hybrids which occur under natural conditions are supposed by Plotnikov to *disappear*; this seems to me to be the weakest point in his argument, and I believe the breeding experiments reported in this paper prove that Plotnikov's "disappearance" can only be interpreted as transformation into the opposite phase, which he so stoutly denies.

Potgieter (1929) states "these facts . . . clearly demonstrate that the phase theory is scientifically unacceptable," but the "facts" upon which he bases this definite conclusion do not bear critical examination. This author's whole discussion of the phase theory suggests that he did not fully grasp its meaning and implications. Thus he measures the hind femora and fore-wings of 19 individuals which were of the *gregaria* type in their immature stages, and attempts to show that their femoral proportions fall mainly in the range given by Uvarov for *solitaria*. Obviously, intermediate forms must occur; even if a long series of specimens showed *gregaria* characters as hoppers and some *solitaria* characters as adults, this would merely indicate that they represented transitional types.

In spite of the final and complete conclusions at which Potgieter arrives, his paper cannot be considered as offering serious criticism of the phase theory.

The phase theory has been mentioned and accepted as a fact by writers like Imms (1930) and Wardle (1929). The conclusions at which Allee (1931) arrives in his book on animal aggregations are of interest as representing those of a critic not directly concerned with entomological problems: "In final criticism of the phase theory, it does not seem to be clearly proved that the transformations from one phase to another do actually take place on a large scale and to a convincing degree. . . . For the time being it must rest with a verdict of unproved but a promising opening for further work."

The criticism of Allee was justified, to a certain extent, because very little actual proof of the transformation of the phases under laboratory conditions has been published. In papers like those of Zolotarevsky (1929) and Johnston (1926), field observations were reported which strongly supported the theory, but there were no records of transformation observed in cages.

The recent paper by Johnston & Maxwell-Darling (1931) brought forward further evidence of transformation of the phase *solitaria* of *Locusta migratoria*, L., into the phase *gregaria*, both in cages and in the field, although the extreme form occurring in swarms could not be reproduced in cages by these workers.

The Species dealt with in this Paper.

Most of the work on which this paper is based was undertaken with the brown locust, *Locustana pardalina* (Walker), which has been the most important species in South Africa during the past twenty years. Some of its forms and variations are represented by the coloured figs. on Plates xiv and xv, and the photographs reproduced on Plates xx–xxiii. Adults of the extreme types of the phases *solitaria* and *gregaria*, taken in the field, are shown on Pl. xx. Pl. xiv, fig. 6 represents the extreme *gregaria* coloration of the hoppers and it is surrounded by *solitaria* types (figs. 1, 5, 7, 8, and 9). Pl. xv, fig. 19 is a type of *gregaria* coloration in which the orange is duller and tends to become reddish brown. The phase *transiens* is shown on Pl. xiv, fig. 2 and on Pl. xv, figs. 22 and 25. Comparing figs. 2 and 6, one sees clearly why the *transiens* forms may be called caricatures of the swarming phase coloration; the black areas are present but broken, and the orange is poor.

Living material of the red locust, *Nomadacris septemfasciata* (Serville), was not obtained until March 1931; therefore only a few observations on this species are included. It is illustrated on Pls. xvi and xxvi. The coloured figs. 27 and 32 show the striking contrast in the coloration of hoppers reared in isolation and those taken in swarms.

Much of the work done on *L. pardalina* was duplicated with *Locusta migratoria*, Linnaeus. This species has a very wide range in its solitary phase, which is represented by the form long known as *Locusta danica*, Linnaeus. The swarming forms occurring in different parts of the world differ considerably in size and in the degree of development of the *gregaria* characters, and on the basis of these differences and their geographical distribution the following subspecies have been recognized: *rossica*, Uvarov & Zolotarevsky (1929), in Central Russia; *migratoria*, Linnaeus, in Southern Russia; *migratorioides*, Reiche & Fairmaire, in tropical Africa and the Far East; and *capito*, Saussure, in Madagascar.

Only the phase *solitaria* of *Locusta migratoria migratorioides* was available for experimental work. It is illustrated in the adult stage on Pls. xxix–xxxi and xxxiii, and in the hopper stages on Pls. xvii, xviii and xix. The striking contrast between the phases *solitaria* and *gregaria* in the shape of the pronotum is shown by the enlarged photographs reproduced on Pl. xxxiii. The hoppers described as *gregaria* resembled those illustrated in figs. 40–43, 52 and 60–61; fig. 51 represents one type of *transiens* hopper, and figs. 35, 37, and 57 are types of the phase *solitaria*.

It is to be regretted that the name of this locust has been given as *Locusta migratorioides*, Rch. & Frm., in the recent papers by Lean (1931a, 1931b) and Johnston & Maxwell-Darling (1931), as if *migratorioides* should be recognized as a species instead of being a subspecies of *L. migratoria*, L. The latter authors have also introduced a further complication by referring to "*migratorioides*" as if it were an extra phase, more extreme than the phase *gregaria* in swarm-type characters.

The fourth species kept under observation in cages in Pretoria was *Schistocerca gregaria* (Forskål). Only the phase *solitaria* was available in the form of adults taken in the field in the districts of Van Rhyns Dorp and Calvinia in the Cape Province (Pl. xxxiv, fig. 181). The phase *gregaria* received from East Africa is illustrated on Pl. xxvi and xxxiv. The hoppers described in this paper as *gregaria* are represented by Pl. xix, figs. 55 and 56, and figs. 53 and 54 represent the phase *solitaria*.

Three species of non-migratory ACRIDIDAE* were used in small series of supplementary experiments. *Sphingonotus scabriusculus*, Stål, was reared in painted boxes. It is very common in the permanent habitat of *L. pardalina*. Experiments in crowding and isolation were undertaken with *Oedaleus nigrofasciatus* (De Geer) (= *gracilis*, Sauss.) and *Acanthacris ruficornis* (F.).

LOCUSTANA PARDALINA (WALKER).

TRANSFORMATION OF *SOLITARIA* INTO *GREGARIA*.

In 1923 the writer (Faure 1923) stated that transformation of one phase into the other occurred regularly in nature. This conclusion was based largely on intermittent field observations, and the available experimental evidence was not conclusive. The occurrence of actual transformation was not accepted by all entomologists in South Africa, and certainly not by most administrative officers concerned with locust

* Unfortunately several different family names have been used in recent standard works for the short horned grasshoppers, *e.g.* Acrididae, Acridiidae, Acrydiidae and Locustidae. I have followed Uvarov (1928) in using the first of these four names.

destruction. It was therefore desirable to undertake further experiments in order to clear up the question as to whether one phase could be bred from another in cages. For these reasons attempts were made to produce the phase *gregaria* out of *solitaria* in three different ways :—

1. Hoppers of the phase *solitaria* were collected in the field, and their progeny were crowded together in cages : Table I.
2. Adults of the phase *solitaria* were taken in the field, and their progeny were crowded together in cages : Table II.
3. Young hoppers of the phase *solitaria* were taken from the field and crowded together in cages : Table III.

The results of these experiments may be judged by two different standards : the coloration of the hoppers, and the biometrical measurements of the adults. The two methods of evaluating the results are treated separately below.

The Coloration of the Hoppers as the Standard of Comparison.

Table I.—Hoppers taken in the Field : Treatment.

The results tabulated here were obtained from individuals of the phase *solitaria* taken in the field as hoppers, mainly in the fifth instar. Immature individuals were collected exclusively, in order to make absolutely certain that the insects were undoubtedly of the solitary phase. In the case of solitary adults taken in the field it might be argued that they could have strayed from some unreported swarm. The hoppers were all typical solitary-phase hoppers, mainly green, grey or grey-brown in colour ; no individuals showing the orange and black coloration of the phase *gregaria* could be found in the vicinity, so that there was no doubt whatever that the hoppers had lived as solitary individuals.

About 100 hoppers were taken near Taungs in the Northern Cape Province during February 1928, on a small area of Karroo-type veld about a mile in diameter surrounded by grass veld. The hoppers were present in fair numbers, but there was no suggestion of swarm formation, and two men worked for an hour and a half to collect about 100 hoppers. A further series of about 100 typical *solitaria* hoppers were taken in April 1928 in the districts of Hope Town and Herbert, Cape Province, and the adjoining district of Jacobsdal, Orange Free State, also on Karroo-type veld and at least ten miles in each case from the nearest incipient swarms of hoppers.

These two lots of hoppers were taken to Pretoria and placed in cages. The resulting adults were isolated, usually one female and one male to a cage, sometimes two pairs in a cage, with a view to obtaining as many egg packages as possible. The eggs were stored in dry sand until September 1928, when they were incubated in wet sand. The resulting hoppers were crowded together into one cage, No. L.p. 138 ; as shown in the Table, 240 survived to 19th October, and of these 42·9% were described as good swarm types.

The hoppers listed in Table I were caught and examined individually, except where the contrary is stated. They were divided into three groups according to coloration, without regard to size or the shape of the pronotum. In many cases intermediate forms were found that could not readily be classified as belonging to the *solitaria*, *transiens* or *gregaria* types, but an earnest attempt was made to classify the hoppers as conscientiously and objectively as possible.

The census was taken just before the most advanced individuals moulted to the adult stage, or as soon as two or three individuals had become adults. In most cases a large proportion, possibly about 40%, of the hoppers were still in their fourth instar at the time of the census. The figures in Table I include all individuals found in the cages. Young adults resulting from hoppers of the swarm type can

PLATE XIV. *LOCUSTANA PARDALINA* (WALKER).

Figure

1 ph. *solitaria* ♂ 5th instar, reared in isolation in galvanized gauze cylinder, L.p. 566/29, 22 xi. 1930. (× 1·5)

2 ph. *transiens* ♀ 5th instar, from cage, 3′ × 2′ × 2½′, containing about 1,600 hoppers, L.p. 255, 14 iv. 1930. (× 1·5)

3 ph. *gregaria* ♂ 4th instar, from cage, 3′ × 2½′ × 2½′, containing about 1,600 hoppers, L.p. 255, 20 iv. 1930. (× 1·5)

4 albino ♀ 5th instar, F_1 generation, L.p. 292/16. 16 iv. 1930 (× 1·5)

5 ph. *solitaria* ♀ 5th instar, from the field, Fauresmith, O.F.S., January, 1930. (× 1·5)

6 ph. *gregaria* ♀ 5th instar, from cage, 18″ × 9″ × 15″, containing about 70 hoppers, L.p. 762, 29 iii. 1931. (× 1·5)

7 ph. *solitaria* ♂ 5th instar, from the field, Fauresmith, O.F.S., January, 1930. (× 1·5)

8 ph. *solitaria* ♂ 5th instar, from the field, Fauresmith, O.F.S., January, 1930. (× 1·5)

9 ph. *solitaria* ♀ 5th instar, from cage, 18″ × 9″ × 15″, containing about 30 hoppers, L.p. 249, 31 xii. 1929. (× 1·5)

10 ph. *gregaria* ♂ adult, to show colour of head and pronotum typical of adult about 4 to 5 weeks old, from a cage, 3′ × 2½′ × 2½′, containing about 360 locusts, L.p. 772, 6 vi. 1931. (× 1·5)

11 ph. *gregaria* ♀ adult, to show colour of head and pronotum typical of young adult up to about 2 weeks after last moult, from a cage, 18″ × 9″ × 15″, containing about 70 locusts, L.p. 762, 21 iv. 1931. (× 1·5)

12 ph. *solitaria* ♂ adult, typical grey-brown, reared in isolation in galvanized gauze cylinder, L.p. 697/8, 30 v. 1931. (× 1·5)

13 ph. *gregaria* ♂ adult, to show mating coloration of adults about 8 weeks old (summer). from cage, 3′ × 2½′ × 2½′, containing 600-800 locusts, L.p 629, 21 ii. 1931. (× 1·5)



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TABLE I.

Progeny of about 200 hoppers of *Locustana pardalina*, all typical of the phase *solitaria*, taken in the field in February and April 1928.

L.p. number	Generation	Parents: L.p. number; crowded or isolated	Size of cage used for hoppers	1st instar hoppers			Census based on coloration of hoppers (mainly in 4th and 5th instars)				
				Total put in cage (approximate)	Colour percentage (estimated)		Date	Total	Percentage		
					Grey	Black			*solitaria*	*transiens*	*gregaria*
138	F_1	taken in field; isolated in cages	18″×9″×15″	400	95	5	19.x.28	240	35·4	21·7	42·9
233	F_2	138 isolated ...	18″×9″×15″	500	95	5	10.iv.29	325	0	0·9	99·1
230	F_2	138 isolated ...	18″×9″×15″	600	93	7	8.iv.29	514	0·6	0	99·4
251	F_3	233; crowded ...	18″×9″×15″	?	?10	?90	19.xi.29	449	0	0	100
252	F_3	233; crowded ...	18″×9″×15″	?	?10	?90	19.xi.29	430	0·5	0	99·5
255	F_3	233; crowded ...	6′×2½′×2½′	?10,000	?5	?95	15/18.xi.29	8,290	0·05	0	99·95
255D	F_4	255; crowded ...	3′×2½′×2½′	3,200	3	97	14.iv.30	1,623	0·06	1·54	98·4
574	F_4	255; crowded ...	18″×9″×15″	280	?5	?95	14.vii.30	186	39·8	26·9	33·3
629	F_4	255; crowded ...	3′×2½′×2½′	?3,000	1	99	8.xii.30	about 700 not caught in hand	0	0	100
622	F_5	255D; crowded	3′×2½′×2½′	?3,000	—	—	20.xi.30	1,701	0·06	0·47	99·47
772	F_6	622; crowded ...	3′×2½′×2½′	450	?10	?90	16.iv.31	362	0·3	5·0	94·7

readily be recognized as such by the coloration of the dorsal aspect of the pronotum, which is yellow with black spots (see Pl. xiv, fig. 11). The progeny of the 200 hoppers taken from the field in February and April 1928 was bred through two generations during each of the summer seasons of 1928–29, 1929–30 and 1930–31. The cages were kept in the outdoor insectary (Pl. xxxv), in order to provide conditions similar to those encountered in the field. While the insects were in their hopper stages the cages were usually covered by means of metal rain-covers (Pl xxxvi, figs. 192 and 196) in the case of prolonged and very heavy rains. When there were adults in the cages the covers were placed over them every evening and whenever rain threatened, in order to keep the soil dry. The females lay readily in soil that is quite dry, and when both moist and dry soil is provided, the majority of the egg packages are laid in the latter. In order to obtain an even hatch of hoppers at a convenient time, the eggs were kept dry. In most cases the eggs were afterwards removed and incubated in wet sand at a constant temperature of about 31°C., but in a few cases they were left in the egg-drawers, wetted, and exposed to the sun to hatch.

An abundant supply of succulent green food was provided at all times; during the summer months this usually consisted of green maize leaves or kikuyu grass, and during the winter and spring we used green barley.

Table I contains two columns of figures indicating the coloration of the hoppers in their first instar. Typically the first instar hopper of the phase *gregaria* is practically black (see Pl. xv, fig. 20), while the hopper of the phase *solitaria* is grey-mottled (fig. 21). In the first, as in other instars, *transiens* types are found; these may be described as grey-black (fig. 22). As a general rule the progeny of adults of the phase *solitaria* are grey in the first instar, but in the cages a small percentage of black individuals were found among them (Table I, L.p. 138, page 303). Similarly, a few grey individuals appear amongst the black hoppers hatching from eggs laid by adults of the phase *gregaria*.

In the F_1 generation there were about 95% grey hoppers and 5% black. In F_2 the proportions were about the same; this may have been due to the fact that the F_1 adults were not kept together in a crowd, but isolated in egg-tin cages (Pl. xxxvi, fig. 191) as the P_1 adults had been isolated. In the F_3 to F_6 generations the first instar hoppers were about 90% black throughout, showing that they were already largely of the swarm type even in the first instar.

Results.

Coming to the results of the censuses, we find that the F_1 gave 42·9% phase *gregaria*, and 21·7% phase *transiens*. The general appearance of this crowd of 240 hoppers was orange and black. In other words, a locust officer or farmer finding a swarm of insects in the field with such a percentage of black and orange types would have no hesitation in describing it as a swarm of *locusts*.

From the F_2 to the F_6 generation the percentage of swarm type hoppers was from 94·7 to 100, except in the case of L.p. 574, one of the F_4 lots, where it was only 33·3. This low percentage in L.p. 574 was primarily due to the fact that the hoppers hatched in cool weather on 10.v.1930, and grew up during the cold weather of May and June, the census being taken on 14.vii.1930. This untimely hatch was due to an accidental wetting of the egg drawers in the cage L.p. 255 on 12.iv.1930, during a sudden rainstorm. The drawers were left out of doors and allowed to dry out in the sun; only a small percentage of the eggs obtained sufficient warmth to hatch, and the resulting hoppers were placed in the cage L.p. 574. The main bulk of the eggs did not hatch until the drawers were re-wetted during the hot weather of October 1930, and the resulting hoppers were numbered L.p.629.

During cool weather the hoppers are not nearly so active as they are in hot weather, and the amount of orange and black coloration varies more or less directly with the amount of muscular activity. This is discussed below under the heading

"Summer and winter swarms." The retrogression of the percentage of swarm type hoppers in L.p. 574 is therefore a direct effect of weather conditions, and should not be interpreted as an indication of inability to develop the swarm coloration under crowded conditions. This is shown by the hoppers in the cage L.p. 629, also F_4 from the same lot of eggs, which hatched in hot weather on 23.x.1930 and were described on 8.xii.1930 as "100% swarm type."

Conclusion.

Table I shows that practically 100% *gregaria* coloration was obtained from the F_2 generation onwards by crowding the progeny of extreme *solitaria* hoppers taken in the field. From the point of view of the farmer and locust officer, this is sufficient to prove that swarms can arise from scattered individuals of the phase *solitaria*. The insects in these "swarms" produced in the cages were not only of the same colour as those found in large swarms on the veld, but some of them were also of the same size.

It will be noticed that there was a large loss of individuals in each of the cages. In most cases the figures in the column "Total 1st instar hoppers put in cage" represent nothing more than very rough estimates; this refers especially to the figures preceded by question marks. In other cases the newly hatched hoppers were actually counted. The reduction in numbers was due to cannibalism, escapes through doors at feeding and cleaning times, and to deaths. Possibly these three causes of losses were of importance more or less in the order in which they are named.

It might be argued that the surviving hoppers which showed the *gregaria* coloration were only those that were black on hatching; or in other words, that the coloration of the hoppers was predetermined and not due to the effects of crowding. The figures for L.p. 233 and 230 show clearly that this could not have been the case: about 90% were grey in the first instar, more than 50% of the total survived at the census, and of these about 99% were of the swarm type, so that many of the hoppers which were grey in the first instar must have taken on the orange and black.

Table II.—Adults taken in the Field.

The data in this table represent the results of a series of experiments which were to a large extent a repetition of those listed in Table I, with this difference: the original parents were taken in the field as adults and not as hoppers. The F_1 flyers were all typical of the phase *solitaria*; they were collected from February to May 1929 in the districts of Prieska, C.P., Hope Town, C.P., and Fauresmith, O.F.S. The density of population of these flyers was estimated as varying from about 10 per man-hour to a maximum of 100 per man-hour; that is to say that one person could see the number of flyers mentioned during a walk of about one hour, but not that he could catch that number in one hour.

Although these locusts were taken in the adult stage, they could without any question be described as adults of the phase *solitaria*, because their size and general appearance were characteristic of that phase, and because there were no swarms of any kind on the farms where they were collected.

The first point of interest in this table is the high percentage (97·17%) of *gregaria* hoppers obtained in the F_1 generation, L.p. 276. Factors contributing towards this result were:—Firstly, the large number of hoppers crowded together; the cage was exactly twice the size of that used for L.p. 138, Table I, but the number of hoppers put in it was 2,280, more than five times the number used for L.p. 138. Secondly, the parent flyers were crowded together in one cage for egg-laying, whereas those of L.p. 138 were isolated. Thirdly, the hoppers of L.p. 276 hatched in October, when the weather is usually a good deal warmer than in September, the month in which those of L.p. 138 emerged.

TABLE II.

Progeny of 141 females and 96 males (adults) of the phase *solitaria* of *Locustana pardalina* taken in the field February-May 1929.

L.p. number	Generation	Parents : L.p. number ; crowded or isolated	Size of cage used for hoppers	1st instar hoppers			Census based on coloration of hoppers (mainly in 4th and 5th instars)				
				Total put in cage (approximate)	Colour percentage (estimated)		Date	Total	Percentage		
					Grey	Black			*solitaria*	*transiens*	*gregaria*
276	F_1	taken in field isolated, but crowded in cages	18″ × 18″ × 15″	2,280	86	14	9.xi.29	1,341	0·15	2·68	97·17
227	F_1	ditto 276 ...	18″ × 9″ × 15″	?	—	—	19.xi.29	167	12·5	24	63·5
249	F_1	ditto 276 ...	18″ × 9″ × 15″	?	—	—	20.xi.29	134	9·7	32·1	58·2
474A	F_2	276 ; crowded ...	18″ × 18″ × 15″	717	14	86	17.iv.30	299	3·1	23·7	73·2
474B	F_3	474A ; crowded	3′ × 2½′ × 2½′	?	?60	?40	21.xi.30	1,305	0·3	4·0	95·7
756	F_4	474B ; crowded	18″ × 9″ × 15″	260	?5	?95	14.iii.31	81	3·7	23·5	72·8
773	F_4	474 ; crowded ...	3′ × 2½′ × 2½′	740	2	98	21.iv.31	378	0·2	1·9	97·9

Comparing the figures for Nos. 227 and 249 with those for 276, we note the effect of the greater concentration in 276; all three lots of hoppers came from the same eggs, with the difference that the first hatchings went into 276 and the later hatchings went into 227 and 249.

The rather high proportion of *transiens* types in Nos. 474A and 756 was probably due to the comparatively small numbers surviving to the census, and to the cooler weather usually experienced in March and April.

Additional data on L.p. 176, not included in Table II, are of interest. The first instar hoppers placed in L.p. 276 were examined rather accurately: 1,953 were described as grey and 327 as black, *i.e.*, about 86 per cent. and 14 per cent. respectively. At the census 1,341 hoppers were recovered, and of these 1,303 were described as being of the swarm type. If we assume, for the sake of argument, that all black hoppers survived, there would remain 1,014 grey hoppers surviving to the census; deducting the 38 *transiens* and *solitaria*, we find that at least 976 of the hoppers that were grey in the first instar must have acquired the orange and black coloration during their development from the first to the third, fourth or fifth instars.

Conclusion.

These results show that as large a proportion as 97 per cent. of hoppers of the swarm type was obtained in the F_1 generation from solitary adults taken in the field, by rearing the progeny in a dense crowd. Many of the insects in L.p. 276 were very small, but in this table the coloration of the hoppers is the only criterion.

Table III.—*Solitaria* Hoppers collected and crowded.

Extreme *solitaria* Hoppers.

Eight experiments are listed, but they fall into two groups. In the first five cases the hoppers were actually living in the field as isolated individuals of the phase *solitaria*, as is clearly shown by the fact that it took an entomologist about 2½ hours to collect 100 to 120 hoppers. The hoppers used in Nos. 763 and 764 were taken from small loose swarms, while those of No. 761 were from a scattered lot of newly hatched hoppers.

It should be noted that the hoppers used in the first five cages were mainly in the third and fourth instars. This is due to the fact that those of the first and second instars are very small and difficult to see and catch. As there are only five nymphal instars, the crowding together of hoppers in the third and fourth stages does not leave much time before the final moult for the effects of crowding to manifest themselves. Nevertheless, in the cage L.p. 740 a marked acquisition of the orange and black coloration developed in 15 days amongst hoppers that were all in the fourth instar when the crowding began: 54 per cent. changed towards the swarm type, and of these 16 per cent. were described as *gregaria* and 38 per cent. as *transiens*.

The experiment No. 742 is of special interest in connection with the problem of the green coloration. Fourteen green hoppers of the fourth instar were crowded into a cage $6 \times 4\frac{1}{2} \times 6$ ins. (fig. 197). After 15 days there were 12 survivors, 2 adults and 10 hoppers in the fifth instar, but there was no green colour left on any of them; one hopper was described as a *transiens* type and the others had all become very dark, grey-black solitary types. Very similar results were obtained from 14 green hoppers crowded in cage 741. Taking the first five experiments together, they show that the *gregaria* coloration made its appearance in two to three weeks after *solitaria* hoppers from the field had been crowded together in small cages. The small crowds in these cages had the general appearance of the loose incipient swarms of hoppers often encountered in the field: a miscellaneous lot showing some good swarm types, some *transiens* types and a greater or smaller proportion of solitary types of different colours.

TABLE III.

Locustana pardalina : hoppers of the phase *solitaria* collected in the field and crowded in cages.

Experiment					Result				
L.p. number	Date started	Origin of hoppers	Number of hoppers and dimensions of cage in inches	Instar and colour of hoppers	Number and instar of survivors	Days after start	Classification of hoppers, percentage		
							sol.	*trans.*	*greg.*
413	18.i. 30	Luckoff, O.F.S., 102 collected by one man in 2½ hours	70 6×4½×6	1st, 2nd and 3rd ; grey and green	38 : 3 adults, 19 5th, 14 4th, 2 3rd	21	34	26	40
739	9.xii. 30	Middelburg, C.P., 120 collected by one man in 2½ hours	36 6×4½×6	All 3rd ; grey-brown	24 : 15 5th, 9 4th	16	71	21	8
740	9.xii. 30	Middelburg, C.P., ditto 739	30 6×4½×6	All 4th ; grey-brown	26 : 1 adult, 25 5th	15	46	38	16
741	9.xii. 30	Middelburg, C.P., ditto 739	14 6×4½×6	All 3rd ; green	10 : 9 5th, 1 4th	15 N.B. type mainly	80 Only o with gr y grey-	10 ne of s een tin black	10 olitary ge, rest
742	9.xii. 30	ditto 739	14 6×4½×6	All 4th ; green	12 : 2 adults, 10 5th	15 N.B. grey-	90 All soli tary ho black,	10 ppers none g	0 reen
763	16.ii. 31	De Aar, C.P., small incipient swarms	180 18×9×15	6 1st, 20 2nd, 154 3rd ; about 10 transiens, rest grey solitary	156 : 109 5th, 40 4th, 7 3rd	19	3	24	73
761	13.ii. 31	De Aar, C.P., scattered lot of grey first instar hoppers	300 18×9×15	All 1st ; grey	202 : 154 5th, 48 4th	32	6	22	72
764	16.ii. 31	De Aar, C.P., small incipient swarms	140 18×9×15	4th & 5th ; 5 transiens, 135 grey	118 : 112 5th, 6 4th	11	9	49	42

I believe the formation of incipient swarms of hoppers comes about in the field more or less as follows, although I have not had the opportunity of observing the process in detail. A certain number of solitary type hoppers occur on a given area. If the population is dense enough, some of the hoppers come close enough together to stimulate one another into jumping activity, and at the same time their strong tendency to gregariousness begins to assert itself and tends to keep them together. At first there is probably only spasmodic jumping, but even if the little group should move for only a few yards in one day, it is bound to acquire more recruits, and

this continues until a loose swarm is formed. Examining such an aggregation at a given moment, we note that some individuals are perfect swarm type hoppers; these would be the insects that had been members of the incipient band for the greatest number of days. The *transiens* types would have joined the group later, and most of the solitary types would probably represent the most recent additions.

It should be added that these loose swarms are generally found to consist of insects in many different stages, and even adults remain with the hoppers, indicating that those of the earlier stages join a procession of older hoppers, and *vice versa*.

Hoppers from incipient Swarms.

The last three experiments in Table III differ from the other five in this important respect, that the hoppers had already come together into loose swarms when they were taken from the field. Those used for Nos. 763 and 764 came from a loose swarm that might have camped for the night on an area 10 yards by 5 yards, but it was impossible to determine whether the swarm had originated from eggs laid close together by congregating adults of the solitary phase, or whether it consisted of solitary hoppers that had formed a band in the manner described in the preceding paragraphs. In any case, the vast majority of the hoppers put into the cages were of the grey solitary type.

In the case of No. 761, the hoppers taken were all in the first instar, and of the grey-mottled type of the solitary phase. They were taken in a net on small patches of very short green grass; they had hardly formed a loose swarm yet, but if left together undisturbed they would probably have congregated into an incipient swarm after a week or two.

In Nos. 761 and 763 young hoppers were used, and over 70% *gregaria* type resulted. In No. 764 the insects had already reached the 4th and 5th instars, and therefore the experiment lasted only for 11 days; there were 42% of the hoppers in the phase *gregaria* at the census.

Conclusion.

The data presented in Table III may be summed up as follows: experiments showed that locusts of the phase *solitaria*, if taken off the veld early enough in their development as hoppers and crowded together in cages, would acquire the coloration of the phase *gregaria* before they reached the final moult.

The Biometrical Study of the Adults as the Standard of Comparison.

Tables IV and V contain the results of biometrical studies which were undertaken to compare the cage-bred material listed in Tables I and II with field material.

The Method of Measuring.

The method of taking measurements was as follows: the dry, pinned specimens were measured by means of a pair of dividers, and the readings were taken to the nearest 0·1 mm., on steel rules. Two rules were used, one divided into 0·5 mm. and the other into 0·2 mm.

The characters studied were the same as those used by Zolotarevsky (1929) in his work on *Locusta migratoria capito*, Sauss., in Madagascar, with the addition of the width of the wing, W. In all the tables of biometrical data in this paper, the symbols used have the following meaning:—

A—length of fore-wing, taken from the notch between the two large veins Sc and R, close to the caudal margin of the pronotum, to the extreme tip of the wing;

W—greatest width of fore-wing, taken half way between the tip of the femur and the tip of the wing ;

F—length of hind femur ;

H—height of pronotum, greatest height taken vertically from the middle of the lower margin to the middle of the dorsal aspect ;

M—constriction of the pronotum, or its " pinch," taken in the deepest spot on each side near the middle of the lateral aspect ;

T—width of the head at its widest point a little dorsad of the mandibles.

The figures in the columns A, W, F, H, M and T are the averages of the measurements of the total number of specimens in the various series (except where otherwise stated in footnotes), arrived at by dividing the sum of the measurements by the number of specimens. In the columns A W, A F, M/T and H T the ratios of the averages to one another are presented.

All the specimens measured were mounted on pins, with their wings folded in the natural resting position.

For all the biometrical work reported in this paper the specimens used were random samples. In some cases, notably the extreme swarm and solitary types of *L. pardalina*, all the available specimens were taken. Where large series were available, the only selection made was to take specimens with unbroken wings and legs. In the case of cage-bred material, every effort was made to take out random samples, but many specimens had to be discarded because their wings had been damaged.

Table IV.—Description of Material.

This table contains the data on nine series of male specimens, numbered from i to ix. Series i consisted of 61 males of the extreme *solitaria* type, taken as isolated individuals in the field in widely separated localities from 1917 to 1931. This series is characterized mainly by their extremely small size, as shown by the average length of forewing A, 27·60 mm., as compared with 41·56 for series ix, the extreme *gregaria* type males.

The specimens of series ii were from De Aar, C.P., February 1931, taken on farms where incipient swarms were being destroyed. The majority of these probably lived in isolation during their immature stages, but some of them must have formed part of the very loose aggregations of hoppers which the locust officers were attempting to destroy at the time. The general appearance of these specimens was that of true *solitaria* males, and the best descriptive term I can suggest for them is " *solitaria* beginning to congregate."

Series iii were from an aggregation of flyers that could be described as a loose swarm ; the swarm probably had not yet undertaken definite migration flights when the specimens were taken, for we found it on the only farm in the neighbourhood on which loose swarms of hoppers were being destroyed. The remaining swarms of hoppers contained a large proportion of good swarm types, therefore it is safe to assume that a large percentage of the adults of series iii had grown up in loose swarms and developed the coloration of the swarm phase.

Series iv were from a loose swarm in the Hope Town district of the Cape Province, taken in May 1931. The Senior Locust Officer for the area reported that he had used poisoned bait successfully in an attempt to kill the scattered flyers. Since the number of adults present was such as to call for destruction, it seems probable that some of the insects may have grown up in loose bands of hoppers. In general the specimens of series iv may therefore be said to fall in the same category as those of series iii.

Series v to viii consisted of specimens bred in cages in the experiments reported in Tables I and II above. The material listed in Tables IV and V and also in Tables

TABLE IV.

Locustana pardalina : Males, averages and ratios of biometrical data Measurements in mm., to 0·1 mm.

Series	L.p. number	Description	Number measured	A	A/W	A/F	M/T	H/T	W	F	H	M	T
i	—	Extreme *solitaria* phase, field material ...	61	27·60	5·236	1·964	·9201	1·236	5·27	14·05	5·63	4·19	4·56
ii	782	*Solitaria* beginning to congregate De Aar, C.P., February 1931	50	30·20	5·279	1·983	·8980	1·221	5·72	15·23	5·98	4·40	4·90
iii	787	Incipient swarm, Droogleegte Jacobsdal, O.F.S., April 1928	35	34·74	5·118	1·970	·8782	1·192	6·79	17·63	6·99	5·15	5·86
iv	786	Incipient swarm, Wildsdraai, Hope Town, C.P., May 1931	35	32·71	5·211	1·998	·8829	1·187	6·28	16·37	6·57	4·89	5·54
v	276	F_1 bred in cages (crowded) from extreme *solitaria* phase	36	36·25	4·815	2·076	·8403	1·122	7·53	17·46	7·02	5·26	6·26
vi	233	F_2 bred in cages (crowded) from extreme *solitaria* phase	50	34·32	4·843	2·008	·8482	1·112	7·09	17·09	6·86	5·23	6·17
vii	255	F_3 bred in cages (crowded) from extreme *solitaria* phase	30	37·59	4·759	2·060	·8072	1·065	7·90	18·25	7·31	5·54	6·86
viii	629	F_4 bred in cages (crowded) from extreme *solitaria* phase	30	37·51	4·925	2·040	·8255	1·081	7·62	18·39	7·21	5·50	6·67
ix	783 784	Extreme *gregaria* phase from migrating swarms 1905–1924	61	41·56*	4·770	2·086	·7739	1·040	8·71	19·92	7·87*	5·86*	7·57*

* A based on 53, M on 59, and H and T on 60 males only.

I and II may be identified by means of the L.p. record numbers. In Table IV the series v to viii are represented as four succeeding generations of cage-bred material, but it should be noted that the F_1 was from one stock (Table II) and the F_2, F_3, and F_4 from another stock (Table I). The reason for this is that we did not kill and preserve sufficient material of all generations of the Table I and II series of experiments.

Series ix was a collection of specimens taken at various times from migrating swarms; it represents the only material of the extreme swarming phase available in Pretoria. Unfortunately larger series were not preserved when large swarms were of common occurrence, and the swarms of adults that were encountered during the last four or five years have all consisted of insects of the *transiens* type. The specimens of series ix were taken in localities as far apart as Potgietersrust in the Northern Transvaal and Graaff Reinet in the Cape Province; all the specimens included in the series did not bear labels indicating that they were taken from large swarms, but the locality and date labels enabled us to determine with reasonable certainty that they were taken from swarms.

Table IV.—Discussion of Data.

The length of the fore wing, column A, serves as an index of the absolute size of the specimens, and is more reliable for this purpose than measurements of the total length from head to tip of wing would be, because the head may be stretched forward too far, or pushed back into the prothorax in dry pinned specimens.

The very small size of the males of the phase *solitaria* is brought out by the figures in column A: 27·60 mm. average wing length, as against 41·56 mm. for the extreme swarm phase. In series ii, *solitaria* beginning to congregate, the average was 30·20, and in series iv and iii, incipient swarms, we found 32·71 and 34·74 respectively, showing that the size of the males gradually increases as the insects pass in the field from an isolated existence to life in swarms.

The parents of the specimens constituting the series v to viii were not measured, for the reason that practically all adults have their wings badly damaged after some weeks of confinement in cages, the wings being eaten, or broken against the wire gauze. It can be safely assumed, however, that the parents of these cage-bred series would have given for average wing length a figure very close to that of the extreme solitary specimens, series i.

Although the specimens of series v to viii were reared under crowded conditions, they all showed a distinct increase in size over the field *solitaria* material. The case of series v is noteworthy: an average wing length of 36·25 for the F_1 progeny of field *solitaria* adults, as compared with 27·60 in series i. In absolute size the males of this series were therefore much nearer to the extreme swarm phase than to the extreme solitary phase; although they had been reared under exceedingly crowded conditions, 1,341 surviving out of 2,280 put into a cage 18 in. by 18 in. by 15 in.

The figures in the column A/W represent the ratio between wing length and wing width; they show a marked difference, 0·466, between the extreme solitary and the extreme swarm series, *i.e.*, the fore wings are relatively narrower in *solitaria* and wider in *gregaria*. The series vii, F_3 generation from field *solitaria* crowded in cages, gave a smaller ratio (4·759) than the extreme swarm phase (4·770). The wing width is the most difficult to measure of all the dimensions, because the membrane is more or less flexible on both sides, and there are no definite landmarks demarcating its widest part; therefore the ratio A/W may not be a very reliable character for the determination of minute differences. All the cage-bred series were closer to the swarm type than to the solitary type in A/W.

The ratio A/F gives an expression of the length of the fore wing compared with the length of the hind femur, and is a guide to the relative length of wing compared with the size of the insect. We find that the wings are relatively longer in the extreme swarm phase, but the difference between the figures for series i and ix is only 0·122, whereas the ratios A/W, M/T, and H/T show differences of 0·466, 0·1462 and 0·196 respectively for these series. This indicates that A/F is of less value as a measure of the difference between *solitaria* and *gregaria* in *L. pardalina* than the other three ratios.

In general, the figures in the column A F show that the relative wing length increases as soon as the insects begin to move together in crowds in the field.

As for the figures in column A/F for the cage-bred material, these show that the crowding resulted in a strong tendency to vary towards the swarm type. The F_1 series came nearest to *gregaria*, with a ratio of 2·076; the F_3 and F_4 were nearer to the swarm than to the solitary type, whereas the F_2 specimens had a larger ratio than any of the series from incipient swarms in the field, but were still nearer to *solitaria* than to *gregaria*.

The ratio M/T represents the degree to which the pronotum is laterally constricted, in relation to the width of the head. The figures show that the phase *gregaria* has the head relatively wider and the pronotum more deeply constricted than the phase *solitaria*. The difference between series i and ix is 0·1462, showing that the ratio M/T gives a greater measure of difference between the phases than the other three ratios.

The field series ii, iii and iv all show a decrease in the M T ratio as compared with the extreme *solitaria*, and the Droogleegte specimens of series iii are further from the solitary type in this respect than those of series iv.

In the three cage-bred series M T shows the same strong tendency to vary towards the phase *gregaria*. The F_2 specimens are nearer to the *solitaria*, but F_3, F_4 and F_1 are closer to the phase *gregaria*, in the order named.

In the ratio H/T, we have the relation between the height of the pronotum and the width of the head; the phase *solitaria* has the pronotum relatively higher than *gregaria*. The difference between series i and ix is 0·196, therefore this ratio shows less divergence between the phases than M/T and A/W, but more than A F. In the column H/T, the field material and cage-bred series show more or less the same variation from the *solitaria* towards the *gregaria* type as in the other ratios, with some differences in the degree of variation. For instance, in H/T the F_1 generation is nearer to the *solitaria* than F_2, whereas in M/T F_1 had advanced further towards *gregaria* than F_2.

Table V.—Description of Material.

This table contains the averages and ratios of the females from the same series of specimens as the males listed in Table IV, and the series bear corresponding numbers in the two tables. The females of the cage-bred F_2 are missing from Table V because only a small series of specimens with whole wings was killed and pinned; being anxious to obtain as many eggs as possible for the next generation, I did not wish to kill many of the females.

The small series v_a is from a migrating swarm of adults which I saw on the farm Blackheath, Herbert district, Cape Province, in April 1928. In flight this swarm of young adults might have been about half a mile long and fifty yards wide. Bands of hoppers consisting of a majority of orange and black individuals were being destroyed at that time on adjoining farms. This Blackheath series can properly be designated as swarm material, because the adults were definitely migrating, but it was a small swarm and in its nymphal stages it would probably have been described as a loose band consisting of a mixture of swarm and solitary types.

TABLE V.

Locustana pardalina : Females, averages and ratios of biometrical data. Measurements in mm., to 0·1 mm.

Series	L.p. number	Description	Number measured	A	A/W	A/F	M/T	H/T	W	F	H	M	T
i	—	Extreme *solitaria* phase, field material ...	68	36·49	5·860	2·023	·9229	1·219	6·23	18·04	7·39	5·59	6·06
ii	782	*Solitaria* beginning to congregate, De Aar, C.P., February 1931	50	38·75	5·747	2·040	·9196	1·224	6·74	19·00	7·70	5·79	6·29
iii	787	Incipient swarm, Droogleegte Jacobsdal, O.F.S., April 1928	34	41·16	5·565	2·037	·8880	1·166	7·40	20·21	8·26	6·29	7·09
iv	786	Incipient swarm, Wiidsdraai, Hope Town, C.P., May 1931	37	37·16	5·657	2·044	·8822	1·155	6·57	18·18	7·48	5·71	6·47
v	276	F_1 bred in cages (crowded) from extreme *solitaria* phase	32	38·75	5·299	2·146	·8482	1·089	7·31	18·06	7·35	5·73	6·75
va	—	Small migrating swarm, Blackheath, Herbert, C. P., April 1928	14	41·15	5·455	2·119	·8728	1·149	7·54	19·42	7·94	6·03	6·91
vii	255	F_3 bred in cages (crowded) from extreme *solitaria* phase	30	41·13	5·228	2·153	·8250	1·075	7·87	19·10	7·88	6·05	7·33
viii	629	F_4 bred in cages (crowded) from extreme *solitaria* phase	30	40·44	5·275	2·119	·8346	1·061	7·67	19·08	7·63	6·01	7·20
ix	783 784	Extreme *gregaria* phase from migrating swarms 1905–1924	66	43·25*	5·209	2·138	·7991	1·041	8·30	20·23	8·15	6·26	7·83

* Based on 50 females only.

Discussion of Data.

Column A shows that the females of the extreme swarm phase were considerably larger than those of the extreme solitary phase, but the difference was only 6·76, whereas the males of the same series in Table IV gave a difference of 13·96. Comparing the two sexes of the same series, the males and females of extreme *solitaria* gave an average wing length of 27·60 and 36·49 respectively, with a difference of 8·89; the corresponding figures for the two sexes of extreme *gregaria* were 41·56 and 43·25, difference 1.69. In other words, the males of the swarm phase are almost as large as the females, but in the solitary phase they are only about three-fourths as large.

The series from incipient swarms showed an increase in size over the females of the extreme solitary phase, the Droogleegte specimens going furthest in this direction. Of the three cage-bred series, the F_1 was nearer to the *solitaria* than to the *gregaria* type, but F_3 and F_4 approached more closely to *gregaria*.

In the ratio A/W the females gave a greater degree of difference between the extreme solitary and swarm phases, namely 0·651, than the males, which only reached 0·466. The incipient swarm series all showed a decrease in the ratio A/W, and all the cage-bred series were nearer to the swarm than to the solitary phase, F_3 coming closest to *gregaria*; in the males this generation gave a smaller ratio than the extreme *gregaria*.

In the ratio wing over femur, A/F, the females gave a difference of 0·130 between the extreme solitary phase series and the F_3 cage series, while the greatest divergence in male series was 0·122, between extreme *solitaria* and extreme *gregaria*. As in the other ratios, the incipient swarm series varied in the direction of the swarm type. The figures for the cage-bred series are remarkable in that both F_1 and F_3 gave a larger A/F ratio than the extreme swarm series.

In the case of M/T, we find that the difference between extreme *gregaria* and *solitaria* amounted to 0·1238, showing that this ratio gave a greater measure of divergence between the phases than any of the other ratios in the females, as it did in the males. But in the males the difference was 0·1462, indicating a greater plasticity in the ratio M/T in the male sex than in the female. The four series from incipient swarms gave M/T ratios lower than that of the extreme *solitaria*, but nearer *solitaria* than *gregaria*. The three cage series, on the other hand, were nearer *gregaria* than *solitaria*, F_3 again going further towards extreme swarm type than F_1 or F_4.

The column H/T contains a striking feature in the relative positions of the series i and ii; the De Aar specimens, already congregating, gave a slightly larger ratio than the extreme solitary series taken in twos and threes in widely separated localities. This is the only case in Tables IV and V where series i did not show the greatest degree of divergence from the extreme *gregaria* phase specimens. As before, the cage-bred series varied strongly in the direction of the swarm characteristics, F_4 going furthest in this direction and all three showing ratios nearer to *gregaria* than to *solitaria*.

Summary of Tables IV and V.

The biometrical data for both sexes of *Locustana pardalina* show certain characteristics very clearly:—

(1) A distinct divergence between the extreme *solitaria* and *gregaria* series of field material, giving a standard of measurement that can be used in the classification of material;

(2) A definite variation towards the *gregaria* characteristics in the case of material taken from incipient swarms in the field;

(3) In the case of material bred in cages under crowded conditions, a strong tendency to develop the characteristics of the extreme *gregaria* phase; a regular progression through the succeeding generations was not found to occur,* but in general the F_3 and F_4 generations went farther towards the extreme *gregaria* type than the F_1 and F_2 series;

(4) In most cases the cage-bred series showed characteristics which were nearer to the phase *gregaria* than to the phase *solitaria*;

(5) The cage-bred series came closer to the *gregaria* characteristics than the material from incipient swarms in all cases but two: in both sexes the specimens from incipient swarms at Droogleegte were larger (wing-length) than some of the cage-bred material, and the females from Blackheath were also larger; but the cage-bred series were closer to the *gregaria* type than the incipient swarm series in all the ratios which are of more value than absolute dimensions.

The question arises: did the cage experiments in crowding the progeny of phase *solitaria* from the field result in the production of the phase *gregaria*? In three cases the cage-bred series gave ratios exceeding in *gregaria* characteristics the extreme phase *gregaria* series: males of F_3 in A/W, and females of F_1 and F_3 in A/F; in all other cases the figures for the cage series did not equal those of the extreme *gregaria* series. The approach to the phase *gregaria* was so close that this conclusion appears to be warranted: the phase *solitaria* was transformed into the phase *gregaria* in the cages. This conclusion is supported by the results in Tables I and II, where it was shown that a *gregaria* coloration of nearly 100 per cent. was obtained in the hoppers of these cage-bred series.

It should be borne in mind in judging these biometrical data, that the insects were bred in small cages, which can only be described as providing exceedingly abnormal conditions when compared with the actual conditions of existence in nature. Elsewhere in this paper the conclusion is reached that excessive muscular exercise brings about the change from the phase *solitaria* to the phase *gregaria*. There is also good reason for believing that the life of both adults and hoppers in swarms has a cumulative effect in producing *gregaria* characteristics through succeeding generations. Assuming that these two theses are tenable at least as working hypotheses, consider the difficulty of endeavouring to reproduce the phase *gregaria* to a nicety of biometrical identity in a cage 6 ft. by $2\frac{1}{2}$ ft. by $2\frac{1}{2}$ ft. In nature the hoppers may not get much more muscular exercise than those confined in cages, for in the cages there is activity that hardly ever ceases while the temperature is favorable. And yet, the quality of the exercise in cages is probably distinctly different; the caged hoppers constantly crawl up the side and drop down again, but their jumping is largely confined to short hops, whereas the hoppers in swarms on the veld progress much farther in one jump and take several long jumps in succession. But consider the possibilities of exercising the muscles of flight in these cages, as compared with the open veld, where swarms of flyers may cover several hundred miles in a couple of days. I believe that the muscular activity of both adults and hoppers is of importance in producing the swarm characteristics; therefore it does not seem probable

* The cage-crowded stocks were bred through two generations per annum in order to get as far as possible during the time available. The hottest weather is usually experienced in Pretoria from October to January, during the period of growth of the first summer generation, and it is usually cooler and more rainy from February to May, the period of growth of the second generation. It is clear from the data for summer and winter swarms, recorded elsewhere, that climatic conditions have a profound influence on activity, and even the density of population could not be determined accurately for the whole developmental period of each generation. It follows that any generation might very easily experience less total activity during its development than a preceding one, and a regular progressive increase in *gregaria* characters should perhaps not be expected, although the parallel series of experiments with *L. m. migratorioides* gave results which went much further in this respect than those on *L. pardalina*.

that exact reproductions of the biometrical dimensions of the extreme swarming forms could be produced in small cages by crowding the progeny of the phase *solitaria*.

Transformation of *gregaria* into *solitaria*.

In a preceding section I have described experiments in crowding the progeny of the phase *solitaria* from the field. Unfortunately it was not possible to carry out a parallel series of experiments to study the transformation in the opposite direction by isolating the progeny of the phase *gregaria* from the field, because no swarms exhibiting the extreme biometrical characteristics of the *gregaria* phase occurred in South Africa during the years 1928–1931, while this work was in progress. Large swarms of hoppers were encountered in various districts during this period, but they were the progeny of flyers of the solitary or *transiens* type, and were destroyed before reaching the adult stage. It would have been possible to obtain material from swarms of hoppers showing nearly 100 per cent. of swarm type coloration, but the transformation of the progeny of such hoppers into the phase *solitaria* would not have been convincing because their parents were very different from the true *gregaria* type in biometrical characteristics. This is clearly shown by the figures for the material from Droogleegte, Wiidsdraai and Blackheath on pp. 311, 314 in Tables IV and V.

Incidentally, this lack of material of the extreme swarming phase affords proof of the transformation of one phase into the other. During the period April 1928 to March 1929, the Government of the Union of South Africa spent about £52,000 on the destruction of *Locustana pardalina*. This amount is very small compared with the expenditure incurred during 1922 to 1926, when more than £300,000 was spent in a single year, but the infestation was confined to a very limited area in 1928–29. Broadly speaking, the whole area subject to invasion is now accessible to and worked over by the locust administration, and I accept as actual fact that the extreme swarming phase did not exist anywhere in Africa during 1928 to 1931. Since the Government spent £52,000 in one season on the destruction of swarms of the *transiens* type, it follows that the true phase *gregaria* which overran the country in 1922–26 must have disappeared.

The disappearance proves transformation: after 1926 the scattered remnants of *gregaria* probably disappeared from the parts of the invasion area not included in the permanent habitat; in the Karroo these remnants survived from 1926 to 1928 as isolated *solitaria* locusts; during 1928–31 the population increased sufficiently to form *transiens*, but energetic destruction prevented the species from reaching the extreme *gregaria* expression.

The Coloration of the Hoppers.

Failing good *gregaria* material from the field, the material available in the cages was used in isolation experiments. Experience soon showed that the term isolation had to be construed absolutely literally; that is to say, each cage must contain only one individual. Under favourable conditions of temperature two or three individuals of the phase *gregaria* kept together in a small cage, or even in a cage 18in. by 9in. by 15in., would often stimulate one another into jumping activity and therefore constituted a kind of "swarm." Therefore the term isolation is used here in the sense of one individual, and only one, in a cage. In addition to the stocks listed in Tables I and II, we had in the laboratory some eggs laid by swarms of the *transiens* type during the winter of 1928 in the Herbert district, Cape Province. The majority of the hoppers from these eggs were black in the first instar. Black being the colour characteristic of the swarm phase in the first instar, these black hoppers and those of the stocks L.p. 255–622–629 and L.p. 276–474–773 were used as material of the phase *gregaria* in the isolation experiments. Roughly, half of the hoppers used were from the field *transiens* eggs, and half from the two stocks listed in Tables I and II.

The hoppers were isolated in many different types of cages for various purposes, as described elsewhere in this paper ; celluloid cylinders on growing grass, wire gauze cages, wooden boxes painted in various colours, and painted wire gauze cages.

Of black hoppers of the first instar, 139 were reared in isolation to the fifth instar ; they were classified in the fifth instar as *solitaria* 135, *transiens* 2, and *gregaria* 2, giving respectively 97·1 per cent., 1·45 per cent. and 1·45 per cent. This means that 135 of the 139 hoppers were of the extreme solitary type, showing many different colours and types of coloration, but no sign of the combination of orange and black that is typical of the phase *gregaria*.

In addition to the hoppers which survived to the fifth instar, about as many more were reared in isolation to the third or fourth instars, but it was not thought worth while to tabulate and analyse these in detail, because the insects had not completed their development as hoppers. In all these cases the same general rule held good : the vast majority of black first-instar hoppers acquired the solitary type of coloration in the second, third or fourth instar.

The change from the coloration of the phase *gregaria* to that of *solitaria* was usually very sudden and complete in black hoppers isolated very early in the first instar ; they would remain black until the first moult, but as soon as the second instar hopper was old enough to show its final coloration it would be definitely of the solitary type, showing a great variety of colours except those typical of *gregaria*. In some cases the colours of the phase *gregaria* persisted into the second, third and fourth instars, and in four cases out of 139 even into the fifth instar, as stated above. If the black hopper were not isolated until it had completed half or more of the first stage, it would usually be described in the second as *transiens* or *gregaria*, and then as *solitaria* in the third or fourth instar.

As controls on these isolations we had the cages containing the crowds from which the isolated hoppers had been taken. In all cases the result was the same : in the crowd nearly 100 per cent. developed the *gregaria* coloration. To quote three examples :

	Crowded				Isolated			
	Total	*sol.*	*trans.*	*greg.*	Total	*sol.*	*trans.*	*greg.*
L.p. 255D ...	1,623	0·06%	1·54%	98·4%	16	100%	—	—
622	1,701	0·06	0·47	99·47	13	100	—	—
772	362	0·3	5·0	94·7	4	100	—	—

Some hoppers of the phase *gregaria* were also isolated in their second instar ; 21 were reared to the fifth instar and classified as follows : *solitaria* 19 or 90·5 per cent., *transiens* 2 or 9·5 per cent. and *gregaria* 0.

These results in the isolation of *gregaria* hoppers of the first and second instars warrant the conclusion that the *gregaria* type of coloration is lost very soon if the hoppers are reared in isolation. Only in exceptional cases was the swarm type coloration retained by isolated hoppers into the fifth instar. On the basis of coloration we may therefore conclude that the transformation of the phase *gregaria* into *solitaria* was definitely shown to take place in the cages. This conclusion is supported by the results of the tests of Mendelian inheritance as a possible factor in determining colour types, which are discussed elsewhere in this paper. Further support is found in field observations which prove that hoppers showing the *gregaria* coloration are never found living as isolated individuals ; if one is found, this is a sure indication that the rest of the swarm to which it belongs must be somewhere in the immediate vicinity.

PLATE XV. *LOCUSTANA PARDALINA* (WALKER).

Figures 14-18; locusts reared in painted boxes.

Figure

14 ph. *solitaria* ♂ adult, reared in box painted aniline yellow,* L.p. 283, 28 vi. 1930. (× 1·5)

15 ph. *solitaria* ♀ 5th instar, reared in box painted white, L.p. 288, 16 vi. 1930. (× 1·5)

16 ph. *solitaria* ♀ 5th instar, reared in box painted black, L.p. 445, 25 iv. 1930. (× 1·5)

17 ph. *solitaria* ♀ 5th instar, reared in box painted aniline yellow,* L.p. 283, 9 iii. 1930. (× 1·5)

18 ph. *solitaria* ♀ 5th instar, reared in box painted deep mouse grey,* L.p. 422, 19 iii. 1930. (× 1·5)

19 ph. *gregaria* ♀ 5th instar, from cage 18″ × 9″ × 15″, containing about 200 hoppers, L.p. 235, 30 xii. 1929. (× 1·5)

20 ph. *gregaria* ♂ 1st instar, from cage containing a crowd, L.p. 254. January, 1930. (× 4)

21 ph. *solitaria* ♀ 1st instar, cage-bred, 9 vii 1930. (× 4)

22 ph. *transiens* 1st instar, cage-bred, 29 v. 1930. (× 4)

23 ph. *gregaria* ♂ 2nd instar, from cage. 3′ × 2½′ × 2½′, containing about 2,000 hoppers, L.p. 629, 9 xi. 1930. (× 4·5)

24 ph. *solitaria* ♂ 2nd instar, from cage containing a crowd, L.p. 254, January, 1930. (× 4)

25 ph. *transiens* 2nd instar, from cage, 3′ × 2½′ × 2½′, containing about 1,500 hoppers, L.p. 474, 2 xi. 1930. (× 4·5)

26 ph. *solitaria* ♂ 3rd instar, from the field, Fauresmith, O.F.S., January, 1930. (× 4)

* Colours according to Ridgway.



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The General Appearance of the Adults.

The majority of the isolated hoppers referred to in the preceding section as having been reared to the fifth instar also reached the adult stage, and differed very strikingly from those constituting the crowds from which they had been taken. As young adults they lacked the yellow black-spotted areas on the dorsal aspect of the pronotum which are characteristic of adults bred from *gregaria* hoppers (see fig. 11). They were invariably very small, especially in the male sex. In size and coloration they could not be distinguished from typical *solitaria* material from the field.

Isolation, Semi-isolation and Crowding.

In addition to the isolations of nymphs of the phase *gregaria*, hoppers showing the characters of the phases *transiens* and *solitaria* in their first instar were reared in isolation under the same conditions. The origin of part of the material was the same as that of the *gregaria* isolations, and in addition some hoppers from various other cages of field *solitaria* material were included. It is not worth while to add a detailed analysis of the origin of all the material used ; the point of importance is the coloration of the hopper in its first instar.

It is possible that 100 per cent. black coloration may have been present in dense swarms of first instar hoppers during the periods of maximum swarm abundance and development of the extreme *gregaria* characters ; to my knowledge such swarms were not critically examined. On the other hand, 100 per cent. grey-mottled may be the rule for first instar hoppers of the phase *solitaria* in the field. In cages, however, I usually found a smaller or larger percentage of grey individuals amongst the black hoppers and a few black or grey-black individuals amongst those hatching from the eggs of *solitaria* adults. The exact separation of the types representing the phases is not always possible ; many intermediate forms occur, as we should expect in such a case, where we are dealing with the variations of one and the same species.

Noting the occurrence of a few black hoppers amongst the greys, and *vice versa*, I isolated a number of each type in order to compare the coloration developed by them under isolated conditions. With the small percentage of exceptions noted above, the result was the same, whether grey, black or grey-black hoppers were isolated ; nor did it make any difference whether the grey hopper came from a crowd of black or *vice versa* : when reared in isolation the hoppers became or remained *solitaria*, and when crowded they remained or became *gregaria*.

The grey hoppers of the first instar reared in isolation to the fifth instar totalled 98 ; they were all described as typical *solitaria* hoppers in the fifth instar. Of the grey-black type 15 were reared in isolation, and here also all were described as *solitaria* in the fifth instar. Adding to the 98 and 15 the 139 black first instar hoppers which survived to the fifth instar in isolation, we find a total of 252 ; of these two were described as *transiens* and two as *gregaria* in the fifth. Comparing these figures with the percentages of *solitaria* and *gregaria* obtained in the crowded cages as listed in Tables I, II and III, we are forced to conclude that crowding produced the *gregaria* type coloration and isolation the *solitaria* type. Further evidence bearing on this conclusion will be found under the heading " Mendelian inheritance," where the progeny of one pair of adults is shown to have produced the coloration of both phases under conditions of crowding and isolation.

In dealing with the extreme conditions of complete isolation and dense crowding, the resulting coloration of the hoppers can be predicted with confidence, if the insects are reared under outdoor conditions in the summer time. The effects of temperature and other climatic factors are discussed elsewhere in this paper. Theoretically it might be argued that any desired percentage of *gregaria* type coloration could be produced by varying the density of the population in a cage of a given size. At the

extremes of the range, it is true that the percentage of *gregaria* does vary directly with the density of the population : 500 hoppers in a cage 18in. by 9in. by 15in. would give 95 per cent. or more swarm type, whereas one hopper reared in this cage would show the *solitaria* coloration. But if four or ten hoppers are reared in a cage of this size, the result is difficult to predict. If the four hoppers are swarm types from a dense crowd, they may continue to be very active in hot weather and show a high percentage of swarm type coloration throughout their development as hoppers. Should the weather be rainy or cool, all four hoppers would probably become *solitaria*.

The following examples from the breeding cage records will serve as illustrations :

Gregaria hoppers, 1st instar, in cages 18in. by 9in. by 15in.

Number put in cage	Number surviving to 5th instar	Classified as			Number of days in cage
		soli-taria	*trans-iens*	*gre-garia*	
3	3	1	1	1	31
3	3	–	–	3	31
5	4	–	–	4	31
5	5	5	–	–	38

These and other conflicting results obtained with small numbers of hoppers in relatively large cages have led to the conclusion that the effects of an isolated existence can be satisfactorily studied only by keeping one hopper and only one in a cage.

Factors which influence the Coloration of the Phase *solitaria*.

Field Observations.

It is a matter of common observation that many species of Acrididae bear a very close resemblance to the colour of the soil or the plants on which they occur. Many striking examples of this may be found in the South African fauna, especially in the Karroo areas which are the natural home of *L. pardalina* in its phase *solitaria*. *Sphingonotus scabriusculus*, Stål, is very common in these areas ; the adults have the underwings blue and black, but when the wings are folded the insects resemble their surroundings to a degree that is almost incredible. They love open stony places ; very often the small pebbles lying on the surface differ in colour from the general colour of the soil, and in such situations many of the adults of this grasshopper show both the colour of the soil and that of the stones to a nicety on different patches of their bodies. In flight the grasshopper is conspicuous enough, but at rest it is often exceedingly difficult to see, on account of its very close resemblance to the background.

The nymphs of *S. scabriusculus* also show very good imitation of the colours of the soil ; they often occur on the patches of white limestone which are characteristic of parts of the Karroo (fig. 106), and on these their coloration is a greyish white speckled with minute black spots ; when at rest they can hardly be distinguished from their surroundings. On other geological formations, such as the shales of various colours, these nymphs are much darker and also show striking resemblance to the backgrounds. The so-called toad locusts of the Karroo, *Batrachotettix* spp., also resemble the soil or stones to a remarkable extent, and many other forms could be mentioned in this connection.

In the case of *L. pardalina* the adults of the solitary phase resemble the colour of the soil on which they live to some extent ; those taken on red soils tend to be reddish grey, those from very light grey soil much paler in colour, and so on. But the adults do not equal those of *S. scabriusculus* in this respect. The nymphs of *L.*

pardalina show a great variety of colour types when living as solitary individuals scattered over the veld ; the types illustrated on the coloured plates give only a very inadequate idea of their variability. Greys and browns are very commonly found, and greens where there is plenty of succulent grass ; occasionally some very brightly coloured types are encountered, with bright pink and purple colours, especially in loose aggregations characteristic of the time of incipient swarming.

In the field I have noted a strong tendency to resemblance of the background in *solitaria* hoppers of *L. pardalina*, especially in the southern Karroo districts of Beaufort West and Laingsburg, where patches of differently coloured soil occur in rather close proximity. Possibly the nymphs do not show quite such striking resemblances in the field as those of *S. scabriusculus*, but the two species do not differ greatly in this respect.

Vosseler (1902) believed that grasshoppers resemble the colour of the soil because the tissues of the newly-moulted insects are very susceptible to the influence of rays or a particular colour reflected by the background. This hypothesis was tested by Eisentraut (1927) on nymphs of *Oedipoda coerulescens* (Linn.), a European species that exhibits striking resemblance to the soil on which it lives. Eisentraut was evidently mainly interested in observing the moults in coloured cages, and his negative results may have been due to the fact that he did not keep the insects on the different colours for a sufficiently long time. He concluded that Vosseler's theory was not applicable to *O. coerulescens*, but that the possibility of imitations after longer exposures to the backgrounds still remained.

In 1921–22 I attempted some cage experiments to test the effect of rearing hoppers of *L. pardalina* on backgrounds of different colours (Faure 1923), but the results were inconclusive. Potgeiter (1929) also reported negative results from tests in which soils of different colours were placed in the cages. In both these series of attempts two errors were made : keeping more than one insect in a cage, and having backgrounds of different colours mainly on the floors of the cages. The objection to the former is that two or more hoppers may constitute a swarm under favourable conditions, and to the latter that the hoppers spend a great deal of time sitting on the sides of the cage which are probably not of the same colour as the soil on the floor.

Experiments with Painted Boxes.

Special cages were used from 1929 to 1931 to test the effects of coloured backgrounds (Pl. xxxviii, fig. 198). The boxes were made of teak ; each compartment measured 9in. by 5½in. by 3½in. on the inside and was provided with a close-fitting lid of ordinary window-glass running in a groove. Sometimes the boxes were divided into two by means of a wooden partition. Air-holes, about half an inch in diameter, were provided in the sides and floor and covered with wire gauze. The wood was painted on the inside with ordinary commercial oil-paints, several coats being applied to provide a good even colour. The dry paint on the wood was compared with the coloured plates of Ridgway (1912) and named according to the tints which they most closely resembled.

The cages were kept outdoors ; during warm weather they were protected by a canopy of calico (fig. 194), because they became too hot in the sun. The hoppers were fed by dropping a piece of green food into the cages twice a day, and the cages were cleaned about once a week. For convenience in feeding and cleaning, the lids were divided into two unequal parts. Only one hopper was placed in a cage.

In this type of cage the hopper cannot get away from the painted sides and floor unless it is able to sit upside down on the glass ceiling. During the first instar the hopper can cling to the glass, but not during the other four ; even very young hoppers were not often found sitting on the glass.

The temperature in the colour boxes was not carefully controlled or recorded because the facilities available were not adequate for such exact experimentation. In very hot weather it sometimes happened that the glass became too hot even under the canopy of calico, resulting in the death of the hoppers, and in cooler weather the hoppers sometimes developed very slowly. In addition, the experiments were carried out not only during the summer months but also for part of the winter. For these reasons the records of the number of days after which changes in coloration were noted are not of much value for purposes of critical comparative study. The object of the experiments was to find out whether the colour of the box had any effect on the colour of the hopper; since the different colours were tested simultaneously in adjoining compartments of the same box, the conditions of temperature and moisture must have been very similar except in so far as the different colours absorbed or reflected more or less of the heat of the sun.

The hoppers used were taken from the living material available in the cages, mainly from the stocks of locusts mentioned in the section on isolations. Some were from parents of the *gregaria* type, others from *transiens* or *solitaria*, but the colour of each hopper was noted and regarded as being of more importance than its parentage.

The hoppers in the colour boxes were fed twice a day in hot weather and usually only once a day in cool weather, but they could not be caught, examined and described more frequently than once in five to twenty days, except in a few cases of special interest when notes were made more frequently. It follows that all the moults were not observed and recorded.

After a hopper had lived in a box of one colour for some weeks and showed a good resemblance thereto, it was often transferred to a different colour; in such a case the same hopper would be counted as two " experiments."

The colour of the hoppers was noted as often as possible. It was not practicable to hold the hoppers in one's fingers next to standard colour plates in order to write minutely accurate descriptions, nor was such detail considered necessary. The decision as to whether a hopper did or did not resemble its background was based on personal estimation, but its colour was described as objectively and critically as possible, and comparisons were often made between hoppers in parallel experiments. The results were classified into four groups, according to the degree of resemblance to the background; none, slight, fair and good. All cases of " good " resemblance should not be interpreted as implying that the colour of the hoppers was exactly the same as that of the box. There was a degree of resemblance which enabled any casual visitor, presented with five or six test tubes each containing one hopper and no label (except a number), to replace the hoppers correctly in the cages from which they had been taken. In many cases, especially in the black cages, the resemblance was so complete that one had difficulty in finding the hopper in the cage.

White.

Ten black hoppers of the first instar, phase *gregaria*, were at various times placed in white boxes: 5 of these were described as showing good resemblance to the background, 1 in the second, 3 in the third and 1 in the fourth instar; 4 were classified as fair resemblances, 3 in the third and 1 in the fourth instar; one showed a slight resemblance to white in the third instar. One of the ten black hoppers had therefore acquired a good resemblance to the white box after one moult, and three after two moults. The number of days after which good resemblances were noted varied from 12 to 46 days.

One grey hopper of the first instar showed good resemblance in the third, after 14 days; another first grey was classified as a " good " in the second instar after 17 days. One *gregaria* hopper of the third instar was described as 5th pale coloured *transiens*. Two fourth instar green hoppers both lost the green colour; one showed

slight resemblance to white in the adult stage, the other good resemblance in the fifth instar. A grey-black hopper of the fourth instar was also tested ; after 28 days it was described as an adult showing no resemblance.

One of the black first instar hoppers, No. 288B, deserves special mention ; in the fourth it was described as speckled grey, but in the fifth it was at first greyish white and then it changed to pale bluish green. This hopper is figured on Pl. xv, fig. 15. It was one of the few exceptional cases in which green hoppers appeared in cages where there was not a constant supply of succulent green food in a moist atmosphere.

Fig. 15 does not represent the colour of a hopper that would have been described as showing good resemblance to the white background. Unfortunately the artist could not undertake to make drawings at all times when good material was available ; therefore the really striking resemblance to white obtained in *L. pardalina* is not figured. Pl. xviii, fig. 46, represents a specimen of *L. m. migratorioides* reared in a white box ; the abdomen on this figure shows what a " good resemblance to white " looked like in this species as well as in *L. pardalina*.

Black.

In the black boxes 8 hoppers were tested. Four were black in the first instar, 2 were classified as showing good resemblance in the fourth and fifth respectively ; one as slight and one showing no resemblance. One grey-black first instar hopper was noted as good in the third after 31 days. Two first greys both gave the result " good " in the fourth and fifth instars. A third instar grey-yellow hopper was noted as having a good resemblance in the adult stage.

A very deep blue colour, darker than the Urania blue of Ridgway was also tested, but the boxes were so dark that they could almost be described as black. Three hoppers placed on this colour gave the following result : 2 were black in the first and were noted as good and fair resemblances in the third and fifth respectively ; one first grey hopper was noted as having a fair resemblance in the adult stage.

Deep Mouse Grey (Ridgway).

In boxes painted grey 10 hoppers were kept long enough to give results. There were 7 black instar hoppers: 6 noted as good, of these 3 in the second in 12 to 14 days, 2 in the third and 1 in the fourth instar ; the seventh hopper was described as showing a fair resemblance in the fourth instar. One first instar grey hopper became dark brown and was therefore noted in the fifth as having no resemblance to the background. A second instar green hopper was put into a grey box and noted as having slight resemblance in the third, and a fourth instar green was also placed in the group " slight " in the fifth.

Aniline Yellow (Ridgway).

In these boxes observations were made on 10 hoppers. Five were put in as black in the first instar and noted as showing resemblance as follows : one good in fourth, one fair in second, two fair in third and one slight in third. One grey-black first instar hopper gave good resemblance in the fifth. Two first greys were noted as good in the third and fourth after 14 and 27 days respectively. One *gregaria* hopper put in as a third instar was described as good in the fifth after 16 days. One fourth instar green showed slight resemblance in the adult stage after 46 days.

Bay Brown (Ridgway).

On this dark reddish-brown colour very striking resemblances to the background were noted. The results obtained from 10 hoppers may be briefly summarised : four

were put in as black first instar hoppers and 3 were noted as good resemblances in the third, fourth and fifth instars respectively, while the fourth hopper showed fair resemblance in the fourth instar. Two hoppers placed in as first grey-black were described as good in the second and third instars after 11 and 18 days. Two grey first instar hoppers also showed good resemblance in the third after 20 and 33 days. One third instar green hopper was noted as a good resemblance in the fifth, and a fourth instar green was also " good " in the fifth.

Experiments with Painted Gauze Cylinders.

In this series of experiments, hoppers were kept in cylinders of galvanized wire gauze, about four inches high, tacked on to boards (Pl. xxxviii, fig. 200). The gauze was painted on the inside and outside, and the boards were painted in the same colours. These cages stood outdoors, on tables, exposed to the weather. The hoppers were fed twice a day, a piece of green food being dropped into the cage. The cages were not cleaned as often as the painted boxes, and sometimes a fair amount of surplus food accumulated on the floors, with the result that the floor-board was entirely covered by the yellowish dry food.

Gauze cylinders painted white, gave practically the same results as the painted boxes : out of 11 hoppers tested, 3 were noted as showing good resemblance to white, and 8 were classed as " fair." Three were black in the first instar ; one was classed as good and two as fair in the fourth. Three grey-black first instar hoppers were all noted as fair. Five grey first instars were used ; two were described as showing good resemblance and three as fair.

In black gauze cylinders 11 hoppers were confined : 10 were classed as showing good resemblance and 1 as showing slight resemblance to the background. Five that were black in the first instar and five that were grey all acquired a very dark coloration described as good resemblance ; the one that developed slight resemblance only was grey-black in the first instar.

Table VI.—Summary of the Experiments on Colours which gave positive Results.

In the boxes and gauze cylinders painted white, grey, black, yellow and brown, about 84 per cent. of the hoppers acquired colours which resembled the backgrounds so closely that the degree of resemblance was described as good (about 60 per cent.) and fair (24 per cent.). In many cases the resemblance was very striking, especially in black and bay brown boxes. In view of the facts that the hoppers were taken from the same or similar stocks, and that they were kept side by side under identical conditions, the results can only be interpreted as proving that a direct effect is produced upon the coloration of isolated hoppers by the colour of the background. As stated above, first instar hoppers of three different phases were used in the experiments and in general the same results were noted in the case of all three. Positive results were not only obtained with first instar hoppers, but also with a few of those that were placed on the painted backgrounds in the third and fourth instars.

The change from one colour to another was in all cases a gradual one, and it was permanent as long as the environment remained the same. There was no suggestion of the sudden changes observed in chameleons and other animals. In several special cases notes were taken every day or two, especially in a parallel series of experiments carried out with *L. m. migratorioides*, and in these we could observe that the change was gradual and not sudden. For instance, a *Locusta* hopper had been placed in a white box in its first instar. In the third it had become very pale, of a dirty white colour, and it was then transferred to a black box. After a few days one could distinctly see that parts of the thorax had become much darker ; this process increased until the whole body was a blackish grey, before the moult occurred. After the moult the insect looked pale for an hour or two, but as soon as its cuticula had

hardened it was seen to be very dark, almost black. During the fourth instar the colour gradually became still darker, and after the moult to the fifth, the hopper was described as pitch black. These observations indicate that the change in colour is not due to the effect of the background on the newly moulted insect while it is in the pre-hardened state, as was suggested by Vosseler (1902).

Some types of coloration, such as some of the browns and yellows, which appeared in the painted cages were quite different from those usually found in the field or in ordinary cages. In other cases the hoppers in painted boxes, even though they might be described as showing good resemblance to the box colour, exhibited a type of coloration almost identical with that seen in other cages in which hoppers were living under more or less isolated conditions. This was especially true of those in boxes painted grey. In experiments on *L. m. migratorioides*, the same agreement was noted, especially between yellow hoppers developed in colour boxes and certain types often seen in cages containing a small number.

The question arises whether this similarity between painted-box types and field hoppers, or those from ordinary cages, invalidates the conclusion that the backgrounds in the painted boxes influenced the coloration. It seems quite reasonable to accept the proposition that the background stimulates and brings to fruition an existing ability to produce a certain type of coloration. This is supported by the fact that certain colours produced no effect on the coloration of the hoppers. On the other hand, the colours of the backgrounds in ordinary cages made of wood and gauze may vary in different parts of the cage, so that hoppers reared in such cages may resemble their backgrounds to some extent, although the resemblance may not be a striking one. Therefore I cannot see any reason for rejecting the above conclusions on the influence of the painted backgrounds on the coloration.

TABLE VI.

The data obtained on the colours which gave positive results—*L. pardalina*.

Colour of background	Type of cage	Hoppers, classified according to degree of resemblance to the background				Total hoppers
		None	Slight	Fair	Good	
White	Box	1	3	4	8	16
	Cylinder	–	–	8	3	11
Black	Box	1	1	–	6	8
	Cylinder	–	1	–	10	11
Urania blue	Box	–	-	2	1	3
Deep mouse grey ...	Box	1	2	1	6	10
Aniline yellow ...	Box	–	2	3	5	10
Bay (brown)	Box	–	–	1	9	10
Totals		3	9	19	48	79
Percentages ...		3·8	11·4	24	60·8	—

The question as to how the hopper may be affected by the colour of the background, whether the stimulus is received by the eyes or through the body wall generally, is discussed in the section on blinded hoppers of *L. m. migratorioides* in painted boxes.

Experiments with Colours on which the Results were largely negative.

In addition to the colours already discussed, seven others were tested in the same way, but the results were largely negative with hoppers of both *L. pardalina* and *L. m. migratorioides*, therefore most of these colours were soon discarded.

Green being one of the commonest colours found in *solitaria* hoppers in the field, this colour was one of the first to be tested, but the results were almost entirely negative. Two different greens were used, a dark shade resembling the antique green of Ridgway and a lighter green like the grass-green. First instar hoppers of the black, grey-black and grey types were placed on both shades of green. Fourteen hoppers were kept on green for periods varying from 14 to 106 days, most of them from the first instar to the adult stage, but a trace of green was noted in only two of these. Both hoppers were reared from the first to fifth instar in grass-green cylinders during the winter months; therefore their development was greatly prolonged, and this may have caused the appearance of the trace of green. In any case, there was so little green on these hoppers, compared with the perfect green types so readily obtained on growing grass, as described below, that these two cases of slight resemblance to green paint may be disregarded.

Eosine pink of Ridgway was also tested on one hopper in a box and on four in gauze cylinders. One black, one grey-black and three grey hoppers of the first instar were reared on this colour to the fifth instar and they remained in the cages from 43 to 68 days, but all five experiments were entirely negative. One first instar black hopper was placed in a box painted tawny olive of Ridgway, and lived in it for 51 days to the fifth instar without showing any resemblance to this colour.

The colour nopal red of Ridgway is the only one in this group which produced one case of resemblance classed as fair. Two black hoppers were placed on this colour: one was reddish brown in the third and brick-red and brown in the fifth instar, showing a fair degree of resemblance; the other was described as a fair *transiens* type in the third and its resemblance to the red regarded as doubtful. One first instar grey hopper showed no resemblance to red in the fifth after 42 days. This red colour was also tried with a piece of red window-glass* forming the cover: one first instar black hopper lived here to the third instar and showed some pink on the legs; therefore it was noted as showing a slight resemblance to the red.

Under blue window-glass I used a pale blue colour resembling the dusky greenish blue of Ridgway: one first instar grey-black hopper was put in this box; in the third it was faintly bluish grey after 18 days, but in the fifth instar it was grey-black, without any blue.

The bay brown colour was also used once under an amber window-glass. A first instar black hopper reared in this box lived to the fifth instar but showed no resemblance to brown.

Two combinations of different colours were also tried, but not until the work was almost coming to an end, so very little was done along these lines. Black and white were used together in one box, in stripes about $\frac{1}{8}$in. wide: two black first instar hoppers were placed on these colours; one was described in the fifth as grey-black with some white stripes and classed as a case of fair resemblance, while the other showed no resemblance to the black and white. One third instar *gregaria* hopper was also tested for 13 days; it was described in the fourth as showing no resemblance to the cage.

The orange and black coloration of the *gregaria* type was imitated in colour boxes by painting black spots on a background of orange rufous of Ridgway. Two black first instar hoppers placed in these cages were both described as *transiens* types, one in the third and the other in the fourth instar. Ordinarily, one should expect such hoppers to have a *solitaria* type of coloration in the third and fourth instars, if they were reared in isolation in the other types of cages. It is therefore

* For notes on the spectroscopic analysis of the various kinds of coloured glass used in these experiments, see the paragraph "Experiments with coloured glass" in the section on *L. m. migratorioides*.

possible that the painted backgrounds may have retarded the loss of the *gregaria* characteristics in these two cases, and the experiment is worth repeating. In the case of *L. m. migratorioides*, two grey first instar hoppers were placed in similar cages, and they did not show any resemblance to orange.

With the exception of green and pink, the colours in this " negative " group were not tested on a sufficiently large scale to warrant definite conclusions. A few experiments were made with hoppers of *L. m. migratoroides* on some of these colours, with the same results. The results with the " positive " group of colours were very striking, and therefore stood in sharp contrast to those in the " negative " group.

In the case of green, I am convinced that this colour will not appear in hoppers reared on green backgrounds. Nopal red may have some influence on the colour ; orange-and-black and black-and-white gave inconclusive results.

The Problem of the Green Hopper.

In hoppers and young adults of the phase *solitaria* taken in the field, bright green colours are very often seen, especially in places where succulent green grass is plentiful. Such green individuals are not entirely green, as the coloured illustrations show (figs. 8 and 26). One finds many different types, some very pale, others bright green ; some have far more green than others, but I have seen no examples of *L. pardalina* hoppers with as large an amount of green on them as the green hoppers of *Nomadacris septemfasciata* and *Schistocerca gregaria* (figs. 27 and 53).

The green hoppers found in the field are not necessarily hidden in grass six or more inches high ; they are often seen on the hard limestone patches (fig. 10) which I regard as the favourite haunt of the phase *solitaria*, and here the grass rarely grows more than a few inches high and usually in tufts with a good deal of bare ground between them. Sometimes I have found isolated green hoppers on patches without any succulent grass between the short Karroo bushes, but it is quite probable that such patches may have had a good deal of grass until a week or so before my visit ; the Karroo areas are semi-arid, and a light shower brings on a quick growth of grass which is often completely withered a week or two later. One should therefore guard against hasty conclusions about the succulent grass which a particular green hopper may have had to eat, if accurate information on the conditions obtaining during the life of the hopper is not available.

In breeding cages I have seen very few green hoppers, except those which appeared in the celluloid cylinders described below. This applies to cages containing crowds, small numbers and single hoppers. Excluding those in celluloid over growing grass, about 600 hoppers were reared in isolation, but less than 10 of these showed traces of green coloration. As stated above, backgrounds painted green also failed to produce green hoppers.

It should be emphasized that the usual method of feeding was to throw cut green food into the cages. In the case of cages containing large crowds it would sometimes be necessary to feed four or more times a day to keep the hoppers well supplied with food. In cages containing a few individuals or one only, the usual rule was to feed twice a day ; in hot weather the insects in such cages would therefore not have access to succulent green food for long, because the food wilts very quickly. It follows that the hoppers kept on growing green food lived under entirely different conditions as regards food supply.

Attempts to produce Green on growing Food.

Short Gauze Cylinders.

The first method was to press wire-gauze cylinders into the soil over young maize or barley growing in boxes, and to confine single hoppers in them. The idea was to have the hopper entirely surrounded by green leaves ; therefore the maize was

allowed to grow up against the roof of the cage and curl down again. The cylinder was about 4½in. in diameter and about 5in. high and was made of grey, galvanized wire gauze.

Twenty-five hoppers were confined in these cages for periods varying from 14 to 77 days ; 16 were black in the first instar when put in, and of these 7 became green while 9 did not, the green colour appearing in the second instar in 2 hoppers, during the third in 2, and during the fourth in 3 hoppers. Of first instar grey hoppers 9 were tested : 4 remained grey while 5 became green, one in the third, one in the fourth, 2 in the fifth instar, and one in the adult stage. Out of the 25 hoppers, 12 became green and 13 remained or became grey. The term grey is used in connection with the experiments on green hoppers in a rather wide sense, to include various shades of grey and brown.

An interesting feature in these experiments was the appearance of several hoppers which were both green and grey to such an extent that one could say that there was evidence of a struggle between the green and the grey : the green parts were distinctly greyish-green and the rest of the body of a shade of grey very closely resembling that of the gauze.

This method proved unsatisfactory in many ways : the maize was scorched by the gauze, and the insects did not thrive well and were sometimes caught between the leaves and the gauze and killed.

Tall Gauze Cylinders.

These cages differed from the short cylinders in size, being about 14 inches high and about 4 inches in diameter. They were placed over dense growing grass about 3 to 6 inches in height. The hoppers had plenty of free space to sit on away from the grass and were often found high up in the cages.* Eight hoppers of the phase *gregaria*, first and second instars, were kept in these cages, one in each cage, for periods varying from 28 to 46 days ; not one of them showed any green colour. Two hoppers of the second instar showing poor green coloration were tested : one lost all its green in 15 days and the other was described after 15 days as half grey, half poor green.

Table VII.—Celluloid Cylinders.

I am greatly indebted to Professor H. J. Quayle, of Riverside, California, for the suggestion to use celluloid for making cages. The use of this material opened up several possibilities which gave interesting results. My problem was to confine the hoppers on growing grass in a cage made of material that would not allow them to crawl up on the sides. Glass was not satisfactory, because hoppers exposed to the sun in glass containers do not thrive and are often killed by the heat. Celluloid answered the purpose very well, and could be made into cages of all shapes and sizes with the aid of acetone.

The cylinders were about 8 inches high and about 3 inches in diameter, and were covered with calico or mosquito netting (Pl. xxxviii, fig. 202). They were pressed into the soil over grass, barley or maize growing in boxes or tins outdoors ; the growing food was watered every day, with the result that the atmosphere in the cylinders was usually saturated with moisture, as shown by the condensation of water against the walls.

In the main series of tests in these cylinders 70 hoppers from various sources were used ; the majority came from the cages containing the crowds listed in Tables I

* My field observations have been of a very hurried and spasmodic nature, but they indicate that the hoppers of the phase *solitaria* do not have the habit of climbing plants : one finds them on the ground or on the short green grass, but not up in the *Pentzia* or other Karroo bushes that may be from about three to about eighteen inches in height. But in cages, they are often seen high up against the sides or on the ceiling of gauze.

and II or from similar material ; 51 became green, and 19 did not, *i.e.*, 72·9% green and 27·1% non-green. The majority of these hoppers were placed on grass in their first instar, but we also tested some older hoppers. The following table summarises the results :—

TABLE VII.

L. pardalina hoppers reared in celluloid over growing food.

Instar and colour when placed on growing food	Became green in instar				Total	Average number of days required to become green	Remained grey	Total green and grey
	2	3	4	5				
1st *gregaria*	4	4	5	1	14	16·4	8	22
1st *transiens*	2	1	1	–	4	16·8	1	5
1st *solitaria*	10	4	6	–	20	11·9	7	27
2nd *gregaria*	–	4	1	1	6	15·3	1	7
2nd brown	–	1	–	–	1	5·0	–	1
3rd *gregaria*	–	–	–	–	–	—	1	1
3rd grey	–	–	2	3	5	19·8	1	6
4th poor green ...	–	–	–	1	1	9·0	–	1
Totals					51		19	70
Percentages					72·9		27·1	

The 51 green hoppers were not all of the same shade of green ; they were classified into three groups according to the degrees of greenness as follows : poor green 18, fair green 4, bright green 29. Many were removed soon after becoming green for other experiments, but some which were poor green in the second or third instar, when left on grass, became bright green in their later instars.

It should be noted that a large proportion of the hoppers became green after one moult, whereas others required three or four moults. The minimum number of days required to become green was 5 days. No hopper became distinctly green before it had undergone at least one moult, although a tinge of green was often noted before the moult.

In general the growing food formed a rather dense mat in the celluloid cages, and at first I thought that this was essential for the production of green hoppers, but experience showed that green also appeared in cages in which the hoppers were not " lost " in the grass, as long as there was enough growing grass to provide a constant supply of food.

The Progeny of green and non-green Parents.

The celluloid cages over growing grass seem to provide ideal conditions for the development of the green colour, and yet only about 70% of the hoppers became green. Could this be due in some way to hereditary factors ? Two green male and two green female hoppers sent in by Mr. S. J. S. Marais from the Orange Free State in January 1930 were mated together, and some of their progeny were reared in celluloid over grass. The progeny were grey in their first instar ; of 9 placed on grass 6 became green, and 3 remained grey to the fifth instar.

In another series the progeny was tested of a pair that had remained grey from the first to the adult stage in celluloid cylinders over growing grass without showing a trace of green colour. Fifteen of the progeny, which were all grey in the first instar, were placed in celluloid over grass : 8 became green (5 bright, 3 fair), and 7 remained grey to the fourth, fifth or adult stage.

These experiments would have to be repeated on a much larger scale before definite conclusions could be drawn, but the two series of tests indicate : (1) that the progeny of green by green do not all become green under suitable conditions, the percentage of green hoppers obtained being approximately the same as in the miscellaneous group of 70 hoppers ; (2) that two individuals which remain grey under conditions which produce many green hoppers, can have progeny of which about 50% still possess the ability to develop the green colour under suitable conditions.

Other Attempts to produce Green.

Having succeeded in finding a method of producing green hoppers, I tried to analyse the factors involved. It seemed possible that the constant supply of green food in a succulent growing condition might be the essential condition, although the results in tall cylinders of wire gauze over growing grass did not appear to support this theory in the case of *L. pardalina*.

In order to provide a constant supply of succulent food without allowing the hopper to sit on the grass and thereby expose itself to the possible influence of the green colour of this background, the following experiment was carried out. Young hoppers were confined, singly, in grey wire gauze cylinders on boards (fig. 200). Into each cage one or more blades of green grass were pushed so that only about one to two inches projected into the cage ; five to ten times a day the grass was pushed in further, as required. The other ends of the blades were kept in a test tube of water, so that the hopper fed on grass that was as succulent as growing grass. It cannot be claimed that these hoppers were literally never without succulent food, but compared with others, in whose cages a bit of grass was dropped twice a day, they certainly had the opportunity to feed almost uninterruptedly.

Nineteen first instar grey hoppers were placed in these cages and kept in them for periods varying from 12 to 40 days ; six were removed in the third instar and one in the fourth, but 12 were kept in until they were in the fifth or adult stage. Not one of these insects developed a trace of green ; instead they remained grey and tended to resemble the grey colour of their gauze cages, just as those fed in the ordinary way. Five of the 19 hoppers were removed from these cages to celluloid cylinders on growing grass in their third instar ; 4 became green and one remained grey.

The Fate of the green Colour under altered Conditions of Environment.

In order to study the factors which favour the development of the green colour, green hoppers were taken from the celluloid cylinders and kept under various conditions.

Wire Gauze Cylinders on Boards.

The hoppers placed in these cages (fig. 200) were fed twice a day only by dropping in a bit of green food. The cages were of grey galvanized gauze, tacked on to the boards, and they stood outside exposed to the weather.

Five bright green hoppers in their fourth instar were placed in these cylinders : two became blackish-brown in the fifth and showed no trace of green ; two were grey in the fifth with a trace of green only, and the last one was described as a fair green in the fifth. A third instar bright green hopper became light-grey in the fourth after 5 days, without a trace of green ; it was transferred back to celluloid over growing grass and after 7 days it was described as bright green in the fifth instar.

Green Backgrounds.

Two bright green hoppers in their second instar were placed in gauze cylinders painted green and fed twice a day only ; they both lost their green completely,

being described as grey-brown in the third and fourth instars, respectively, after 10 days. Replaced in celluloid over growing grass, both hoppers were noted bright green again after 10 days, in the fourth and fifth instars.

A second instar hopper noted as a fair green was put into a box painted green and covered with green glass, and was fed twice a day only; it was described as brown in the fifth, having lost all its green colour.

Boxes painted in various Colours.

Here the same painted boxes were used which had served for the resemblance experiments described above. The hoppers were fed twice a day only.

In bay brown boxes three bright green hoppers were tested, one second, one third and one fourth instar; they all lost the green completely after one or two moults, and two showed a fair resemblance to the brown box.

One green hopper in the second instar (poor) was placed in a white box with a single layer of fresh green leaves on the lid; it lived to the fourth instar and was then described as dirty white without any green. A fourth instar bright green hopper was put in a white box without the covering of green leaves; it also became "dirty white, without green" in the fifth.

One fourth instar hopper, fair green, was kept in a box painted aniline yellow; in the fifth it was described as "poor green."

In boxes painted deep mouse grey, two green hoppers were tested: one had no green at all after one moult, the other only a trace of green on the pronotum; both were described as grey after the moult.

Of the 8 hoppers placed in these painted boxes, 6 definitely lost the green colour and 2 showed a strong tendency to lose it.

A moist Atmosphere.

Six green hoppers were placed in celluloid cylinders covered with calico and standing in soil; both the soil and the covers were watered several times a day. The cages stood outdoors exposed to sun and rain. The hoppers were fed by means of blades of grass kept in bottles of water, as described above. All of these six hoppers retained their green colour through two to three instars for periods varying from 17 to 42 days.

Two other green hoppers of the second instar were kept in glass lamp chimneys on wet soil and covered with calico; they were fed by means of a piece of green food thrown in twice a day. This was done during cool weather in April–May 1931, therefore the glass remained cool enough and the food remained more or less succulent for most of the day. Both these hoppers remained green, one to the fourth and the other to the fifth instar.

Eight hoppers were therefore tested in a moist atmosphere with a more or less constant supply of green food; all of them retained the green colour. This was not the case in a parallel series of tests with *L. m. migratorioides*, where 9 out of 12 hoppers lost the green colour.

A dry Atmosphere.

In this series the hoppers were placed in celluloid cylinders on dry sand covered with mosquito netting. They were fed by means of blades of grass standing in tubes of water. The cages were kept outdoors under a canopy of calico, to avoid excessive heating of the sand in the sun, as this would have killed the hoppers on hot days. Four bright green hoppers were tested: two in the second, one in the third and one in the fourth instar. The fourth instar hopper remained green through the fifth; the other three hoppers lost their green completely after one or two moults.

Various other Tests.

Two bright green hoppers of the third instar were placed in celluloid cylinders on the bright red flowers of *Canna indica* without any other food. The stems of the flowers were kept in water so that the atmosphere in the cylinder was more or less saturated. The cages stood under a canopy of calico. One hopper had lost all its green after one moult in 7 days; it was returned to grass under celluloid and became pale green again in the fifth after 32 days. The other hopper was described as poor yellowish-green in the fourth instar after 26 days.

On the yellow flowers of a cultivated *Coreopsis* a bright green hopper of the second instar was tested; it was described as yellowish-green in the fourth.

These three hoppers fed on food devoid of chlorophyll in a moist atmosphere definitely showed a strong tendency to lose the green colour. Similar results were obtained with hoppers of *L. m. migratorioides*.

In a gauze cylinder painted bright red (Nopal red of Ridgway) we placed a bright green hopper of the fourth instar and fed it on blades of grass kept in water. After 9 days it was in the fifth instar and noted as a fair green; 14 days later, it was a very poor green, and 4 days after that it was noted as bluish-grey with a slight trace of green. This is of interest because it shows the gradual loss of the green colour between two moults.

Finally, a green hopper of the fourth instar, described as a poor green, was placed in a cage containing a crowd of hoppers of *L. m. migratorioides*; after 9 days it was noted as a good *gregaria* type.

General Conclusions on the Green Colour.

Certain preliminary conclusions which can be drawn at this stage may prove interesting and stimulating, although one realizes that the solution of the problems involved in the nature of the green and other colours lies in the field of exact biochemical work.

It is evident that the green colour stands in a class by itself. Whereas grey, yellow, brown, black and dirty white were developed in imitation of the colour of the environment, green was not obtained in hoppers kept on green backgrounds. The albino race showed no tendency to acquire the *gregaria* coloration or to imitate the background, but 5 out of 11 albinos became green on growing grass.

Although 100% of the hoppers did not become green in them, the celluloid cylinders over growing food enabled me to produce green hoppers at will. In these cages there were: (a) a very moist, if not saturated, atmosphere; (b) an abundance of green succulent food; and (c) an absence of predominating background colours other than that of the green leaves. These three factors are undoubtedly present to a greater or lesser degree in the field under conditions where many green hoppers occur: the atmosphere is quite moist, especially at night, in the microclimate in which the insects live, surrounded by green leaves; there is an abundance of tender green grass after good rains; and if we assume that the hoppers remain on the grass for a large part of the day while feeding, they would not be greatly subjected to the influence of the colours predominating on the bare patches.

Assuming that these three factors together constitute the conditions necessary for the development of the green colour, let us test this hypothesis by examining the results obtained with green hoppers kept under various conditions.

The experiments showed that the green hopper lost its green very soon if it was transferred to a wire gauze cylinder and fed only twice a day; here the atmosphere was much drier, the food soon wilted, and the grey background provided by the gauze was strongly imitated by the hoppers.

Similarly, all three factors were absent in the painted boxes which had a drier atmosphere, food twice a day only, and backgrounds of colours readily imitated. In the case of the cages painted green, we had proof that the green background did not influence the colour of the hopper at all, because green hoppers lost their green in these cages. This suggests that the green background provided by the grass is not a factor in the production of green, unless we assume that the organism is very sensitive to shades and qualities of green.

The only cages in which green hoppers remained green were those with a moist atmosphere: here plenty of green food was supplied in a succulent condition to hoppers in celluloid on wet sand. It should be noted that the third factor—absence of colour to imitate—was lacking here, because the sand was either greyish-white or reddish-brown, two colours which are sometimes imitated. It is true that the blades of grass used in feeding projected into the cage for 1 to 2 inches, so that the colour of green leaves was also not entirely eliminated.

The tests with green hoppers in a dry atmosphere indicate that green only develops in the presence of a rather high degree of moisture. The sand forming the floor was kept dry and doubtless served to keep the atmosphere rather dry. Plenty of green succulent food was provided, but the blades of grass did not usually project into the cage for more than 1 to 2 inches.

In the tests with succulent plant food devoid of chlorophyll, a moist atmosphere was present; the yellow colour of *Coreopsis* would be imitable, but it is doubtful whether the red of *Canna* should be classed as such. There was a strong tendency to lose green, and this was definitely confirmed by more extended tests on green hoppers of *L. m. migratorioides*.

The one green hopper placed in a red gauze cylinder, and fed on grass standing in water, lacked a moist atmosphere; the red colour was not readily imitable.

The failure to produce green hoppers in grey gauze cylinders in which succulent green food was available most of the time was probably due to the relatively dry atmosphere and the strong influence of the grey colour of the gauze. The same probably applies to the tall gauze cylinders over growing grass in which no green hoppers appeared; here the hoppers may have spent most of their time on the grey gauze above the grass where the atmosphere would be much drier than in celluloid cylinders over growing grass, and where they were subjected to the stimulus of the grey colour.

Finally, we come to the possible influence of hereditary factors on the production of green hoppers. Under the most favourable conditions, only about 70% of the insects became green, both in the F_1 progeny of green parents, and in miscellaneous hoppers of which the parentage was not known in detail. Two parents which had remained grey under the most favourable conditions for green, gave progeny of which about 50% became green. My tests with the progeny of known parentage were not extensive enough to warrant the drawing of conclusions, but all the experiments on *L. pardalina* and *L. m. migratorioides* taken together indicate the possibility that heredity plays some part in determining whether a hopper can become green or not. It should be clearly understood, however, that any studies of hereditary factors on these insects must be carried out with due regard to the environment in which the hoppers are reared: if they are not strictly isolated, the *gregaria* characters will develop; if the conditions of food and moisture are not favourable, green will not appear, whether the problematical hereditary factors are present or not.

To sum up, it appears that the two factors which are definitely involved in the production and retention of green are an abundant supply of succulent green food and a moist atmosphere. Possibly the absence of a background colour which is readily imitated may also be of importance, and the hereditary factors may play a part in determining whether a hopper has the ability to become green.

Is Chlorophyll present in the Tissues of the Green Locusts?

In view of the close association between an abundant supply of green succulent food and the green colour, it seemed worth while to test for the presence of chlorophyll in the tissues. I am indebted to my colleagues, Drs. C. E. B. Bremekamp, H. G. W. J. Schweickerdt and V. Voss for undertaking the following spectroscopic and chemical tests which showed that there was no chlorophyll, as such, in the tissues.

Two tests were made, one in March and the other in May 1931, in which the following green material was used :—

(1) *L. m. migratorioides*, 4 hoppers, 2 in fourth and 2 in fifth instar ; *L. pardalina*, 2 hoppers in fifth instar.

(2) *L. m. migratorioides* only, 29 specimens : 3 were in third, 9 in fourth, 14 in fifth instar, and 3 were flyers.

The same procedure was followed in both cases. The specimens were killed in a cyanide bottle, and the alimentary canal was completely removed from each one to eliminate the green leaf tissue which it might contain. The material was then dried in an oven at 96°C. for 2 hours, powdered, and extracted with 50 cc. of 85% acetone in water. After filtration the extract, which was of a golden-yellow colour, was poured into 40 cc. of petrol ether in a separating funnel, and 100 cc. of distilled water was added. After thorough shaking this mixture separated into two layers, the petrol ether taking up the pigments, while the water dissolved the acetone. The water was run off and the washing process repeated several times to remove the acetone. The petrol ether layer was cleared by treatment with anhydrous sodium sulphate, filtered and examined spectroscopically.

A layer 15 cc. in thickness showed an absorption band with its centre at 6,700 Angstrom, but no other bands could be observed. After evaporation to half the original volume, the same absorption band became broader and more distinct, but no other bands could be found. Nor was there any trace of the red fluorescence characteristic of chlorophyll solutions.

The petrol ether extract was then saponified by means of 30 cc. of 30% KOH in methyl alcohol. After a few minutes water was slowly added, but the watery layer remained clear and colourless, showing that chlorophyllides evidently had not been formed.

Several Changes in Coloration during the Development of one Hopper.

Table VIII.

The coloration of the nymphs of *L. pardalina* is determined by the conditions obtaining in their environment : in crowds the *gregaria* coloration develops, and the colours of *solitaria* hoppers are determined by those of the background or by the food and moisture. If the conditions are radically changed, the hopper will usually also change its coloration after one or two moults. Theoretically, it would therefore appear to be possible to produce a definite change of coloration after each of the first four moults, if the insect were transferred to a different environment at the right time.

Let us take the following hypothetical case : starting with a black first instar hopper, it is placed in isolation on growing grass on the day of hatching ; after the moult to the second instar it is green, and about the second day of this stage, as soon as the green is well defined, it is transferred to a brown colour box ; about two days after moulting it shows a distinct resemblance to brown and is placed on growing grass again ; in the fourth instar it has once more become green, and is transferred to a black box ; after the moult to the fifth it is distinctly blackish-grey and gradually becomes darker until the colour is described as a fair resemblance

to black at the end of the fifth stage. There have therefore been four distinct changes in coloration.

The records do not show that four complete changes were actually observed during the development of any hopper, but many cases exactly like this hypothetical one could be observed if one had the facilities for detailed work of this kind.

During the course of the work many hoppers were transferred from one type of cage to another, but no serious attempt was made to reach the maximum number of changes. Notes could not be written on each cage every day, and the transfers were therefore often made too late in an instar to make possible a change of colour after the next moult, because it takes several days for the new environment to influence the coloration sufficiently to bring about a change. The notes in Table VIII show that each of the three first hoppers had two distinct changes in coloration, and that the last two each changed colour three times. It is possible that No. 675 had four changes, because the majority of the hoppers in the cage from which it was taken were grey in the first instar.

TABLE VIII.

Hoppers of *Locustana pardalina* that changed colour two or more times as a result of altered conditions of the environment.

L.p. number	1st instar	2nd instar		3rd instar		4th instar		5th instar	
	Colour	Colour	Days	Colour	Days	Colour	Days	Colour	Days
547	black	yellowish-grey Y	19	grey-yellow Y	35	dark grey-brown B	8	black-brown B	34
610-634	black	not noted C	—	not noted C	—	green C	18	reddish-brown A	41
614-635	grey	not noted C	—	not noted C	—	green C	18	dirty yellowish-white W	27
546-609	grey	reddish-brown A	11	green C	11	green A	5	reddish-brown A	46
675	probably grey R	*gregaria* type R	—	green C	7	grey N	5	green C	7

The figures in the columns " days " refer to the number of days after which the colour was noted, counting from the date on which the environment was changed. The capital letters in the columns " colour " refer to the various conditions :—

A.—In box painted teak brown (bay of Ridgway).
B.—In box painted black.
C.—In celluloid cylinder over growing grass.
Y.—In box painted yellow (aniline yellow of Ridgway).
W.—In box painted white.
N.—In galvanized gauze cylinder 4in. by 4in. on board ; fed twice a day only.
R.—In crowded cage with other hoppers (L.p. 564).

NOMADACRIS SEPTEMFASCIATA (SERVILLE).

This species is known in South Africa as the red or red-winged locust. It occurred in vast migrating swarms at various times from about 1893 to 1909, and was particularly troublesome along the east coast, although it is also remembered by the

inhabitants of the Karroo and Orange Free State as the " new " locust of 1896. After the summer of 1909–10 nothing was seen or heard of this species until swarms made their appearance in Northern Rhodesia about 1929. In December 1930 swarms migrated from the north into Ngamiland in the northern part of the Bechuanaland Protectorate and oviposited there. The writer is indebted to the Union Department of Agriculture and its Locust Administration for living material forwarded to Pretoria during the campaign conducted against the hoppers in Ngamiand early in 1931.

In the November 1924 number of the Journal of the South African Department of Agriculture, there is a statement to the effect that scattered flyers of this species had been observed in September at Nelspruit in the Transvaal. No specimens were taken, and it is probable that the large grasshopper *Ornithacris cyanea* (Stoll) was reported as " the red locust " on account of its brightly coloured hind wings.

In July 1930, the writer visited Nelspruit and Barberton, and went on to Lourenço Marques and Vila de João Belo (Chai Chai) in Portuguese East Africa in search of specimens of this species, but no trace of it could be found, although *Ornithacris cyanea* was present throughout the Low Veld.

While he was in the Kalahari with the Vernay-Lang expedition, Mr. G. van Son took one specimen of this species near Tsotsorogo Pan in Ngamiland between June 17 and July 9, 1930.

Nomadacris septemfasciata is readily recognized, as pointed out by Uvarov (1928), because the reticulations on the basal part of the fore-wings are finer and denser than in any other locust of like size (Pl. xxviii, fig. 121). It is a large, long-winged species (Pl. xxvi, fig. 112), the largest of the four species of migratory locusts occurring in Southern Africa, and is distinctly red in colour in the young adult state (Pl. xvi, fig. 33). The hind-wings become purplish pink at the base when the adults are about three or four months old, hence the name red-winged locust.

Very little is known about the permanent habitat of this species, but it will in all probability be located in swampy regions overgrown with dense tropical vegetation near rivers or lakes in Central Africa. Its invasion area is known to extend from the South-Western Cape to the Congo and Abyssinia, but it does not appear to breed permanently anywhere in the Union of South Africa.

The Hoppers.

The hoppers of the phase *gregaria* are beautifully coloured creatures with a general appearance that suggests neatness and agility (Pl. xvi, figs. 31 and 32). In cages they have the habit of jumping neatly through the air from one side of the cage to the other, and there is a strong tendency to hide under leaves and other objects ; these habits suggest that the species is strongly phytophilous. They were found to be less active than those of *L. pardalina* and *L. m. migratorioides*. Roughly estimated, the *Nomadacris* hoppers show an activity of about 60% in cages, if that of *L. pardalina* hoppers is described as 100%, and the former only become very active at relatively high temperatures.

Description of the Hopper in the fifth Instar Phase *gregaria*.

Measurements.—Total length about 40–45 mm., width about 6–8 mm. ; pronotum length on dorsum 9–10, length at base 5 mm. ; length of wing-pad 13–16, width 5 mm., extending to middle of the fourth segment of the abdomen ; hind femur length about 20–24 mm., width near base 4 mm. ; antennae length 13 mm.

Colour.—Head : labrum, mandibles, clypeus and frons up to a line passing just in front of the eyes, dark orange ; eyes dark brownish red ; vertex and genae almost wholly black, vertex duller, tinged with orange, genae shining black ; an oblique

PLATE XVI. *NOMADACRIS SEPTEMFASCIATA* (SERV.).

Figure

27 ph. *solitaria* ♀ 5th instar, caught in laboratory garden (escaped from cages), N.s. 38, 3 iv. 1931. (× 1)

28 ph. *transiens* ♀ 4th instar; was swarm type in 3rd, isolated in celluloid over growing grass, 28 ii. 1931, killed and painted 15 days later, N.s. 11. (× 1·5)

29 ph. *gregaria* ♂ 4th instar, showing reduction of black on gena and pronotum, from a crowded cage, 8 iv. 1931. (× 1·5)

30 ph ? *solitaria* ♂ 5th instar, from field, Ngamiland, Northern Bechuanaland, February, 1931. (× 1·5)

31 ph. *gregaria* ♀ 3rd instar, from swarms, Ngamiland, February, 1931. (× 1·5)

32 ph. *gregaria* ♂ 5th instar, from swarms, Ngamiland, March, 1931. (× 1)

33 ph. *gregaria* ♀ adult, from swarms, Ngamiland, April, 1931. (× 1)



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yellow band just under the eye ; a small triangle on the lower anterior margin of gena is orange about like the face ; on the hind margin of gena there is a line about 1 mm. by 2 mm. extending dorso-cephalad that is orange in colour with small yellow markings.

Antennae.—Basal 3 mm. brownish ventrally, rest black ; dorsally only about 2 mm. paler at base, rest black. Maxillae and labium pale brownish orange, last segments of palpi black, penultimate of maxillary palpi also blackish.

Pronotum.—The dorsal, pitch black, median line about 2 mm. wide (measured from above), extending the full length of the pronotum ; measured from the side, it is about 1 mm. wide, the lower margin somewhat irregular. General colour of pronotum laterally yellow, tinged with grey ; there is an irregular black spot about 3 mm. by 1·5 mm. about 1 mm. from lower margin and 1 mm. from anterior margin ; about 20 small black dots below this and about 20 above it in the anterior half, and a marginal series of black dots along the cephalic, ventral and caudal margins of the yellow area.

Mesothorax.—Episternum dull, reddish brown ; epimeron dorsally black, then paler, blackish-brown.

Metathorax.—Dorsal half black, lower half light reddish-brown. Base of wing pad black, veins black, rest of wing pad light grey.

Abdomen.—Dorsal median black line on segments 3–8 about 2 mm. wide, measured dorsally, about 1 mm. wide measured laterally ; sides of abdominal segments 2–8 with irregular yellow markings on a black background, as illustrated (Pl. xvi, fig. 32) and a white line less than 0·5 mm. wide on the lower margin of the tergites ; segments 9, 10, 11, cerci and podical plates largely brownish-orange like face.

The *ventral aspect* of the thorax coloured about like the face only duller, with many brownish specks ; abdomen ventrally yellowish-grey, with numerous minute grey specks.

Fore and Middle Legs.—Coxa and femur orange-brown, with minute blackish specks ; tibiae similar, with black specks but more black than orange, and mesotibia black in distal third, yellow anteriorly, tarsi almost wholly black above.

Hind Leg.—Coxa pale orange ; femur brownish-orange, with numerous black and yellow specks, orange-brown at tip ; there is a black band about 3 mm. in length on the femur, followed by a yellowish area.

Hind Tibia.—Distal fourth black, basal three-fourths yellow-brown to reddish-brown with black dots ; rows of tibial spurs variable, mainly yellow with black tips. Tibial spurs and tarsal claws black. Tarsi black dorsally, yellow ventrally.

As in the case of *L. pardalina* and *L. m. migratorioides*, the hoppers of the second, third and fourth instars are very similar in coloration to those of the fifth in the phase *gregaria* (Pl. xvi, fig. 31). Even in the first instar, *Nomadacris* hoppers have the general pattern of markings that is found in the later instars.

The Phase *solitaria*.

Very little is known about the solitary phase of the red locust. Uvarov (1924 and 1928) recognized the locust formerly known as *Acridium coangustatum*, Luc., as being very close, morphologically, to *N. septemfasciata* and assumed that it represents the phase *solitaria* of the latter. The single specimen brought by Mr. van Son from Ngamiland probably represents the phase *solitaria*, because it was the only specimen seen at a time when no swarms were known to be present in Bechuanaland. It is paler in colour than the adults from swarms, being brownish-grey, and is also distinctly smaller ; in addition, its wings are relatively shorter compared with the length of the hind femur. If this specimen is typical of the phase *solitaria*, there is much less difference between the adults of the two phases in this species than in *L. pardalina* and *L. m. migratorioides*.

Isolation on growing Food.

Eleven of the hoppers of the phase *gregaria*, received from the field, were placed in isolation in celluloid over growing grass or barley, with the result that 9 became green and 2 did not acquire any green coloration. Fig. 28 (Pl. xvi) represents a hopper that was a good *gregaria* type in its third instar like fig. 31 ; after 15 days in isolation on growing food it had lost all the orange and most of the yellow, and a great deal of the black had become much paler. Fig. 27 shows the next stage in the loss of the *gregaria* characters in which the only remaining black was a dull blackish mid-dorsal line on the abdomen, a greenish-black line under each eye, and some minute black specks ; this represents a hopper that escaped and was later caught in the garden close to the cages.

Of the 11 hoppers placed on growing food, 4 were in the second instar at the start : 3 had become green when they reached the fifth instar, but one showed no green and was described as "light brown, with no orange, *gregaria* pattern black recognizable, poor *gregaria* type." Four hoppers were put on grass in the third as good *gregaria* : 3 became green and 1 had no green and no orange but enough black to be called "poor *gregaria* type." Three were in the fourth, *gregaria*, when put on grass, and all three became green. Unintentionally the experiment was repeated with hoppers which escaped into the garden ; 5 of these were recovered and all were largely green.

Most of the hoppers described as green in the preceding paragraph were not so green as fig. 27 ; they retained distinct traces of the black pattern of the phase *gregaria*, but these were less distinct than the black on fig. 28.

To the writer's great surprise, there was no green whatever on 7 adults obtained from green hoppers ; instead these adults were red and grey, very similar to the one figured (fig. 33) but with the red and brown both a good deal paler.

Other Isolations.

About 15 hoppers of the third instar, *gregaria* type, were isolated in wire gauze cages and fed twice a day only. These lost practically all the yellow and the orange of the phase *gregaria*, and the parts so coloured became a dull, brownish-grey. A good deal of the black characteristic of the *gregaria* pattern remained recognizable in all the hoppers, but it was dull brownish-black, instead of bright black. Fig. 29 shows a type of head found in a number of the *gregaria* hoppers on arrival from the field ; this appears to be the first part of the black pattern to disintegrate in isolation, although it may also be a variation within the bounds of the phase *gregaria*.

Four hoppers were isolated from the third to the fifth instar in gauze cylinders painted black and four in white cylinders. Here the result was a distinct tendency to become paler on the white and darker on the black background, but the imitations were not so distinct as those obtained in *L. m. migratorioides* or *L. pardalina*. On both black and white the *gregaria* pattern remained distinctly recognizable ; in white cages the black markings were dull, brownish-grey, in black cages they remained a good black. The parts that are yellow and orange in *gregaria* showed distinct imitation of the white and black backgrounds, being respectively whitish grey-yellow and dull grey-brown.

Evidently the black markings, characteristic of the phase *gregaria*, are not so easily lost in this species as in *L. pardalina* and *L. m. migratorioides*, but the majority of the hoppers reared in isolation had already reached the third instar when they were isolated.

The adults obtained in these isolations were all smaller than the *gregaria* adults from the field and paler in coloration, but they had a certain amount of reddish coloration, when still young adults, suggesting the red of fig. 33.

Fig. 30 represents a hopper of the fifth instar taken by Major Blignaut in Ngamiland while he was on the campaign against the swarms of hoppers. It was found in the motor-car ; therefore one could not tell whether it had come from a swarm or not. Since there were no specimens like this one, amongst many hundreds of *gregaria* hoppers received in Pretoria, it seems safe to assume that it lived in isolation at least for a part of its life on the veld. In general, the hoppers isolated in cages resembled fig. 30, except that they usually had dark markings on the pronotum and hind femur, and less distinct black markings on the abdomen.

The Adults.

The hoppers received in their third instar early in March became adults towards the end of April. At first there was a bright red coloration on the head, pronotum and legs of young adults received from swarms in the field, but this gradually faded, until these parts were brown after a few months. In the cages, we did not obtain such bright red specimens as that represented on fig. 33.

The purplish pink colour did not appear at the base of the hind wings until about August. Copulation and egg-laying occurred from September to November in locusts kept outdoors and in those kept in a glass house (not artificially heated) during the winter months. These observations therefore confirmed the statements of Lounsbury (1909) and others that there is a long imaginal diapause during the dry season in this species and that it has only one annual generation.

LOCUSTA MIGRATORIA MIGRATORIOIDES, REICHE AND FAIRMAIRE.

Known distribution in South Africa.

The subspecies *migratorioides*, Rch. & Frm., of *Locusta migratoria*, L., attracted a great deal of attention in Nigeria, the Sudan and East Africa from 1929 to 1931, because it appeared in these areas in large migrating swarms. In South Africa we know it only in its phase *solitaria*, which has a very localised distribution although it occurs in widely separated localities. It occurs at Stellenbosch in the South-Western Cape Province, according to Dr. C. K. Brain, and it is common along the Olifants River in the Van Rhyns Dorp district, Western Cape. There are also records of specimens taken in the last few years at Brandvlei, Calvinia district, and on a farm near De Aar, both in the Cape North West. From Heilbron district, Orange Free State, Dr. T. J. Naudé brought me some specimens ; we took one female in Pretoria, and Mr. G. van Son found several specimens at Lake Ngami in 1930 on the Vernay-Lang Kalahari Expedition.

It is possible that this locust may have occurred in swarms in South Africa in former years, but it seems safe to assume that the presence of swarms of considerable size would not have escaped official notice during the last thirty years. There is a published record of two specimens " caught from a straggling swarm " by a farmer in the Wodehouse district of the Eastern Cape Province in March 1909 ; one of these was forwarded to London and identified at the British Museum as *Locusta danica*, L. (Lounsbury 1910). We have no very conclusive evidence to show that the whole swarm really consisted of individuals of this species. The second suggestion of the occurrence of a swarm of this species that has come to my notice was a statement made to me verbally by the late F. Thomsen, formerly a Government locust officer ; on seeing hoppers of the swarming phase in our breeding cages, Mr. Thomsen thought he recognized them as a strange type of hopper he had seen in small numbers in the Rustenburg district somewhere between 1910 and 1920. Unfortunately there are apparently no records of this occurrence.

In 1921 a complaint was received from a farmer near Klaver, C.P., on the Olifants River mentioned above, about the phase *solitaria*, which had become abundant enough to damage the fodder grass on his lands. In December 1928 and January 1929, I went to Klaver and vicinity to collect living material, and brought to Pretoria about 40 pairs of adults taken in the fields of lucerne grown there under irrigation. From about 15 December 1930 to 15 January 1931, Mr. B. van Zyl collected about 400 adults for me at Vredendal, near Klaver.

The Van Rhyns Dorp district is very hot desert country with a rainfall of possibly 5 to 8 inches per annum and a desert scrub type of vegetation. In the irrigated lucerne lands *L. m. migratorioides* probably finds a microclimate that is characterised by considerable heat and high humidity. Yet it does not appear to find the conditions favourable for excessive multiplication or variation in the direction of the phase *gregaria*.

The habits of this locust stand in direct contrast to those of *L. pardalina* ; the latter is a lover of open spaces, while the former hides in the dense growth of lucerne and is exceedingly difficult to catch, mainly because it gets down near to the ground and hides. B. van Zyl reported that he found it in greater numbers in weedy (*i.e.*, grassy) fields of lucerne.

At Brandvlei I found this locust in the stubble of recently cut wheat lands. In the De Aar district it was taken in maize lands—small irrigated patches in the semi-arid Karroo—but not on the open veld where *L. pardalina* occurs.

I have no details about the conditions under which it occurs at Stellenbosch, but this is in the winter rainfall area of the Western Cape. The other two localities, Heilbron and Pretoria, are in the summer rainfall area, grass veld where there is usually plenty of green grass during the summer months.

Transformation of *solitaria* into *gregaria*.

Source and Treatment of Material.

In view of the absence of swarms of this species from South Africa, I felt that it would be interesting to crowd the progeny of the phase *solitaria* in cages in order to study the coloration, and the biometrical data on adults, as in the work on *L. pardalina*. In this case I took adults only, because I could not find enough hoppers in the short time at my disposal ; in any case, there could be no foundation for an objection to the effect that the locusts might have come from swarms. The field material was so scarce at the time that it took two of us three days to catch about 40 pairs of adults, so that the conditions under which they lived can only be described as typically solitary. The P_1 adults from the field were isolated, in pairs, in egg-tin cages, and their progeny crowded together, but the F_1 adults and those of all the succeeding generations were kept together, under more or less crowded conditions, for egg-laying on egg-drawers.

The egg packages of this locust are laid only in moist or wet soil, and should be kept rather moist to ensure a good hatch ; therefore it is difficult to remove the packages without breaking them. The eggs of *L. m. migratorioides* were usually left *in situ* in the soil of the cages. In the beginning the egg-tins were placed in incubators, but for later generations the tins and drawers were left outdoors.

The locusts in the cages listed in Table IX (p. 344) received the same general treatment as that described for the series of experiments with *L. pardalina* (Tables I and II), except that the cages were not so frequently covered to keep out the rain. In taking the results it was not practicable to catch out the specimens and examine each one individually in all cases, therefore the percentage of *gregaria* and other types was sometimes merely estimated.

We found this locust very easy to breed in cages with a minimum of attention. The progeny bred from the 40 original pairs increased at such a rate that we had to discard many of them in the F_3 and F_4 generations. Plenty of succulent green food, and the soil in the egg-drawers kept moist, are the two conditions which favoured its successful breeding in the cages kept outdoors.

General Notes on Development and Behaviour.

The details of its life-history were not carefully noted, but the following points may prove of interest.

The females lay more than one egg package; in a series of about 30 females kept in cages, each with one male only, 2 laid 11 packages each, 3 laid 9 each, 6 laid 8 each, and a number laid 4–6 packages. In cages containing 5 to 20 females, with about as many males, on egg-drawers we also found that an average of about 2 packages had been laid per female. The eggs only rarely are laid in dry soil, the females showing very great preference for moist soil: in a cage containing a crowd of adults, one drawer was kept dry, the other wet; after five days 40 packages had been laid in the wet soil and only one in the dry soil.

The eggs cannot be stored for long periods at ordinary room or outdoor temperatures, like those of *L. pardalina*; they will either hatch or die. Hatching was obtained in the case of some eggs stored for about 6 months at a temperature of about 15–20° C. and then placed in an incubator at about 31° C. If the eggs are placed in an incubator at 31° C. about a week after they are laid, they will hatch in 10–14 days. Outdoors in the drawers of the cages, they hatch about 3–4 weeks after they are laid in warm weather.

The total period required for the development of the five immature stages is about 8–10 weeks. Two generations per annum was the general rule in the cages kept outdoors. Starting with adults collected in the field in December 1928 and January 1929, we had the adults of the F_1 generation from April to June 1929. These adults survived the cold weather and laid their eggs in September; these hatched in October and the F_2 adults appeared in December 1929 and January 1930. The same order of events was repeated in 1930 and 1931. If left undisturbed, the generations would become confused in the cages, because the adults live for many months; therefore we cleared out the old adults when their progeny were approaching the winged state.

In general, the behaviour of the hoppers of this locust in cages may be said to be very similar to that of *L. pardalina*. In cages containing crowds the hoppers are very active at favourable temperatures, but they do not jump quite as actively as those of *L. pardalina*. If a score-card based on general impressions is drawn up and the jumping of a crowd of *L. pardalina* is called 100% activity, then that of *L. m. migratorioides* would probably be given a "score" of 80% under the same conditions.

Differences between the Phases.

The morphological differences between the adults of the solitary and swarming phases of this subspecies are very striking, especially in the shape of the pronotum, which bears a highly arched dorsal carina in *solitaria*, while it is concave and lacks a carina in *gregaria*. The wings of *gregaria* are relatively longer, its head is broader, and its pronotum is more deeply constricted than is the case in the phase *solitaria*. These differences will be discussed under the heading "biometrical study."

In coloration, the young adults of *gregaria* are yellowish-grey, with black lines on the dorsal aspect of the pronotum; later the general colour becomes darker, more brown, and the black lines fade away. At sexual maturity the males show a striking yellow coloration, as illustrated (fig. 44).

In the phase *solitaria*, the adults vary considerably in coloration. In the green lucerne fields near Klaver, C. P., B. van Zyl collected 415 adults, of which 233 were green, or 56·1%, and 182 grey or brownish, or 43·9%. The colour was distributed among the sexes as follows: green: 141 females, 92 males; grey: 55 females and 127 males. Near Brandvlei, C.P., we found a preponderance of light straw coloured adults in the wheat stubble. The yellow colour of *gregaria* males was never seen in solitary males in the field or in cages.

The coloration of the hoppers of the phase *solitaria* proved to be exceedingly variable in cages, as the coloured illustrations show on Pls. xvii, xviii and xix. In the field I found only a few hoppers, and they were green and grey. The *gregaria* hoppers of the European form of *L. migratoria* have been described and figured by Uvarov (1928) and other authors; the form which occurred in the Federated Malay States was described and figured by Pratt (1915), and Zolotarevsky (1929) published coloured illustrations of the subspecies *capito* of Madagascar. The hoppers of *L. m. migratorioides* phase *gregaria* were described from the Sudan by Johnston and Maxwell-Darling (1931).

In crowded cages in Pretoria, hoppers were obtained which resembled those described from other areas as phase *gregaria* very closely. Figs. 40–43 and 52 (Pls. xvii and xviii) represent the types which were classified as *gregaria* in the censuses listed in Table IX. In this work the fifth instar hoppers with a rather broad dorsal median line of orange on the pronotum (broader than in fig. 41) were classed as *transiens*. Material kindly sent by Mr. W. V. Harris from swarms in Tanganyika, after most of the work was completed, showed that the East African swarm hoppers all had this orange on the dorsum of the pronotum.

The black on the pronotum of the Pretoria hoppers had more of a velvety appearance than a sooty black, and in almost all cases there were blue markings on the lower or anterior margins (or both) of the black (fig. 40).

In the third and fourth instars the *gregaria* hoppers are very similar to those of the fifth, but in the second there is much less orange and more grey-black. The material of the first instar from East Africa (preserved in alcohol) was distinctly grey-black, speckled, a good deal darker than the *solitaria* hopper figured (Pl. xix, fig. 62), but not nearly as black as figs. 60 and 61. Mr. Harris wrote that he had observed no black forms in the swarms, but these were reported from the Sudan by Johnston and Maxwell-Darling. Pl. xviii, fig. 51 represents an interesting type of *transiens*, where the orange has been replaced by green, while a great deal of the velvety black is still present.

The Coloration of the Hoppers as the Standard of Comparison.

Table IX (see p. 344).

This table contains the results of a representative selection of censuses taken in cages containing the progeny of the 40 pairs of adults from Klaver, C.P. It shows that more than 95% of the hoppers in cages containing large crowds developed the orange-plus-velvety-black coloration even in the first generation, in spite of the fact that the P_1 adults had been isolated for egg-laying. The lowest percentage of *gregaria*, 26·1%, was found in a cage containing only 46 hoppers.

A very interesting feature was the appearance of some practically pitch black hoppers of the first instar in several cages; these were F_3 hoppers and they appeared amongst the progeny of parents and grandparents that had been densely crowded in the F_1 and F_2. Only one of these cages, No. 132B, is listed in Table IX. Black hoppers also appeared in the F_4 and F_5 generations. These hoppers (figs. 60 and 61) were actually blacker than the progeny of large migrating swarms of adults in Tanganyika. Their appearance was the more striking because all the hoppers

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35	ph. *solitaria*	♂ 5th instar, ing only abou
36	ph. *solitaria*	♂ 5th instar, 5 hoppers, u Solitary type
37	ph. *solitaria*	♀ 5th instar from cages),
38	ph. *solitaria*	♀ 4th instar about 12 hop
39	ph. *gregaria*	♂ 2nd insta about 100 ho
40	ph. *gregaria*	♀ 5th insta about 500 ho
41 42 43	ph. *gregaria*	5th instar, 1930. Diffe hoppers of s
44	ph. *gregaria*	♂ adult, fro 400 locusts, in ♂ ♂ abou

of the F_1 and F_2 had been uniformly pale grey-mottled (fig. 62), no sprinkling of black individuals having been found as in the case of *L. pardalina*.

I regard the occurrence of the black hoppers of the first instar as very important additional proof of the transformation of the phase *solitaria* into *gregaria*.

A number of these black hoppers were taken from various cages early in the F_5 generation and placed together in the cages L.d. 564 and 566, which are listed at the end of Table IX. This process of selection introduced other factors in addition to those involved in crowding, but it was not applied to all the cages, therefore the unselected material of F_5 served as a control. The hoppers in the two selected lots were individually examined when the majority were well advanced in the fifth instar, and in both cases 100% were of the *gregaria* type. The unselected F_5 material was not examined in the same way, but the percentage of *gregaria* in them was also very high. There was no noticeable difference in size or coloration between the selected and the other hoppers or adults, although the biometrical comparisons showed interesting variations, as will be seen later.

Winter and Summer Crowds.

No definite attempt was made to breed *L. m. migratorioides* in the winter months for comparative studies of the effects of temperature on the production of the phase *gregaria* as was done in the case of *L. pardalina*. Some lots reared under crowded conditions were, however, examined in June and July, and two of these are included in Table IX. Broadly speaking, there did not appear to be much difference in the percentage of *gregaria* coloration found in similar concentrations during the hotter and cooler months. Speaking from general impressions, I would also suggest that the *gregaria* coloration appears more readily, that is, in crowds of lesser density and as a result of a lower degree of activity, in *L. m. migratorioides* than in *L. pardalina*.

General Conclusions.

Judged solely on the coloration of the hoppers, the crowding of the progeny of phase *solitaria* resulted in the production of nearly 100% phase *gregaria* from the first to the fifth generation. The type of coloration described as *gregaria* in these experiments had a very close resemblance to specimens from large swarms from East Africa; the cage-bred material differed only in having a larger amount of velvety black. Velvety black is not found in *solitaria* hoppers in combination with orange, therefore this excessive blackness of the cage-bred material might with more justice be described as an ultra-swarm character than as a tendency towards the solitary type.

First instar hoppers, practically pitch black in colour, made their appearance in the cages, and this is regarded as important additional proof that transformation to the phase *gregaria* had been accomplished.

The Biometrical Study of the Adults as the Standard of Comparison.

Material and Methods.

The material listed in Tables X and XI (p. 346) consisted of eleven series of specimens. Series i were taken at random from the 415 adults collected at Vredendal, C.P., during December 1930 and January 1931; these represent the extreme phase *solitaria*. Series ii, iii and iv were the progeny of the 40 pairs of adults taken in the same locality in December 1928 and January 1929, crowded in cages; the specimens measured were random samples taken from cages L.d. 41, 45 49 and certain others of the same parentage. Material from the same stock is listed in Table IX. Series from the F_1, F_3 and F_5 generations only were measured, because time and facilities were limited.

TABLE IX.

Locusta migratoria migratorioides: Progeny of about 40 pairs of the phase *solitaria* taken in the field near Klaver, C.P., December 1928 to January 1929.

L.d. number	Generation	Parents: L.d. number; crowded or isolated	Size of cage used for hoppers	1st instar hoppers: Total put in (approx.)	1st instar hoppers: Colour: percentage estimated: grey	1st instar hoppers: Colour: percentage estimated: black	Census based on coloration of hoppers: Date	Total	Percentage: *sol.*	Percentage: *trans.*	Percentage: *greg.*
44A	F_1	Taken in the field and isolated in cages	18″×9″×15″	51	100	—	6.iv.29	46	47·8	26·1	26·1
41		do.	do.	180	100	—	22.iii.29	156	12·2	32·7	55·1
57		do.	do.	108	100	—	30.v.29	127	1·6	13·4	85·0
58		do.	do.	406	100	—	30.v.29	254	0·8	3·1	96·1
49		do.	do.	800	100	—	3.vi.29	424	—	4·5	95·5
100	F_2	60 & 63; crowded	do.	?	100	—	23.xii.29	87	—	2·0	98·0
44B		44; ,,	do.	—	—	—	23.xii.29	135	17·8	5·9	76·3
132A		106 etc.; ,,	18″×18″×15″	1,005	100	—	20.xi.29	424	1·0	6·0	93·0
133A		106 etc.; ,,	18″×18″×15″	2,000	100	—	20.xi.29	659	1·0	2·0	97·0
69	F_3	69; ,,	18″×9″×15″	800	—	—	8.iv.30	36	—	—	100·0
133B		133; ,,	do.	300	—	—	8.iv.30	64	—	10·0	90·0
132B		132; ,,	do.	400	90	10	8.iv.30	100	—	5·0	95·0
45A		45; ,,	3′×2½′×2½′	—	—	—	25.iv.30	±1,900	—	—	±100
45	F_4	45; ,,	do.	500	100	—	1.xii.30	450	2·0	2·0	96·0
50A		50; ,,	do.	—	—	—	1.xii.30	600	1·7	3·2	95·1
45B	F_5	45; ,,	do.	3,000	—	—	16.iv.31	±2,000	—	—	±100
50B		50; ,,	do.	—	—	—	24.iii.31	1,000	±4·0	±2·0	±94·0
564	F_5	Black 1st instar hoppers selected from crowded cages 309, etc.	18″×9″×15″	280	—	100	8.v.31	97	—	—	100·0
566	F_5		do.	164	—	100	5.vi.31	70	—	—	100·0

Series v were the adults reared from the black first instar selection described above. Series vi and vii represent the most extreme *gregaria* material available, taken from large migrating swarms in Tanganyika Territory. The two lots were measured separately to give some idea of the variations, and combined as series viii for convenience in having one set of figures for comparison with the cage-bred and field *solitaria* material.

Series ix is of considerable interest. In September 1923 some swarms of moderate size were reported in the neighbourhood of Makoni, in the east of Southern Rhodesia; specimens from these were identified at the British Museum in London as *L. m. migratorioides*. Mr. R. W. Jack, Chief Entomologist for Southern Rhodesia, kindly sent me some specimens, and a few more were obtained through the Department of Agriculture in Pretoria. Unfortunately no more than 9 males and 6 females were available, so that we could not measure the same numbers as in the other series. There was no widespread invasion of any part of Africa by this locust in 1923 to my knowledge, so that the Makoni material does not represent the extreme swarming phase such as it occurred in East Africa in 1931, but it came from swarms of fair size, as the records of the Department in Salisbury show. It is of great interest to compare the measurements of series ix with those of the Tanganyika swarms and the cage-bred specimens.

Series x and xi are from some specimens kindly forwarded to me by Mr. H. B. Johnston from the Sudan; x from migrating swarms and xi the cage-bred progeny of phase *solitaria* from the field. The specimens of series xii are some F_5 locusts from L.d. 49 and other cages, each one reared in a cage by itself during the F_5 only.

The method of taking measurements and the symbols used are exactly the same as in the case of the data on *L. pardalina* in Tables IV and V (pp. 311, 314), except that the width of wing W, and the ratio A/W were omitted in this case as being of no value in describing differences between the phases.

Table X.—Males.

In absolute size, as represented by the length of fore-wing A, the Tanganyika males of series viii were larger than those of any other series. Makoni males came next and the F_5 black hopper selection third with an average of 41·22, followed closely by the extreme *solitaria* F_5, F_3 and F_1, in the order named.

Turning to Table XI, compare the absolute size of the two sexes in the same series. The differences between the fore-wing lengths of females and males are: extreme *solitaria* 12·8, F_1: 7·38, F_5: 5·78, F_3: 5·59, Makoni 5·15, F_5 black selection: 4·83 and extreme *gregaria* 2·31. In the large migrating swarms the males are nearly as large as the females, but the extreme *solitaria* males are much smaller. The F_5 black selection series came closer to the extreme *gregaria* condition in relative size of sexes than the Makoni specimens.

The ratio A/F is of greater value as an expression of the difference between *solitaria* and *gregaria* in *L. m. migratorioides* than in *L. pardalina*. In Table X we find a difference between series i and viii of 0·346, whereas the corresponding difference in *L. pardalina* was only 0·122. The greatly increased relative length of the wings is readily seen in the phase *gregaria* of *L. m. migratorioides*, even on casual examination. The F_1 series in Table X A/F came nearest to the extreme *solitaria* with a ratio of 1·887; then going up towards the *gregaria* ratio, we find Makoni, F_5, F_3 and F_5 black selection, in the order named, showing that even the F_3 generation had relatively longer wings than the Makoni swarm material. The Makoni series, with a ratio of 1·987, is nearer the *gregaria* than the *solitaria* type. The F_5 black selection came very close to the Tanganyika swarms with a ratio of 2·102, as compared with 2·115, and if we consider the series vi separately, the cage-bred series gave a greater wing-ratio than the series from swarms: 2·102 as against 2·097.

The ratio M/T expresses the relation between the constriction of the pronotum and the width of the head. Comparing the differences between the extremes for the two species, we find that *L. pardalina* gave 0·1462 and *L. m. migratorioides* 0·1235, indicating that the ratio M/T is of more value in the former species. Arranging the figures under M/T in a series according to their numerical values, we find that the F_5 black selection, 0·8143, is the only one nearer to *gregaria* than to *solitaria*; F_1 is closest to *solitaria*, with F_3, Makoni and F_5 tending away from *solitaria*, in the order named. Here both the F_5 series exceed the Makoni swarm specimens in *gregaria* characters.

In the ratio H/T we have a measure of the height of the pronotum as compared with the width of the head. It is of more value here than in *L. pardalina*, and comes second in *L. m. migratorioides* only to the ratio A/F. The very high, arched pronotum of the phase *solitaria* is a conspicuous feature differentiating it from the phase *gregaria* (see Pls. xxxi and xxxiii). The difference between the extreme *solitaria* and *gregaria* is 0·303. Arranging the figures in numerical order, we find that F_1 is the only series nearer to *solitaria* than to *gregaria*. The other series all come nearer to *gregaria*, the F_5 black selection going farthest in this direction, followed by F_5, Makoni and F_3, in the order named.

TABLE X.

Locusta migratoria migratorioides, males: Averages and ratios of biometrical data. Measurements in mm., to 0·1 mm.

Series	L.p. number	Description	Number measured	A	A/F	M/T	H/T	F	H	M	T
i	568	Phase *solitaria*, Vredendal, Van Rhyns Dorp, C. P., Dec., 1930—Jan. 1931	100	41·03	1·769	·8819	1·305	23·19	8·18	5·52	6·26
ii	41 etc.	F_1 crowded, in cages, from *solitaria*	50	39·80	1·887	·8630	1·190	21·09	7·28	5·28	6·12
iii	45 etc.	F_3 crowded, in cages, from *solitaria*	50	40·24	2·008	·8404	1·135	20·04	7·03	5·20	6·19
iv	49 etc.	F_5 crowded, in cages, from *solitaria*	67	40·27	1·996	·8217	1·093	20·17	6·88	5·17	6·30
v	564	F_5 black 1st instar selection, crowded in cages from *solitaria*	30	41·22	2·102	·8143	1·053	19·61	6·76	5·22	6·42
	566		20	50·48	2·097	·7636	1·020	24·08	8·35	6·25	8·18
vi	572	Migrating swarms, Tanganyika, May 1931	30	48·99	2·128	·7549	·9896	23·02	7·90	6·03	7·98
vii	570	Migrating swarms, Tanganyika, March 1931	50	49·59	2·115	·7584	1·002	23·44	8·08	6·12	8·06
viii	572	Migrating swarms, Tanganyika, Nos. vi and vii combined									
	570		9	45·67	1·987	·8346	1·109	22·98	7·82	5·89	7·06
ix	—	Migrating swarms, Makoni, Southern Rhodesia, 17.ix 1923	4	48·95	2·059	·7523	1·012	23·78	8·18	6·08	8·08
x	—	Migrating swarms, Sudan, 1930	7	42·86	1·874	·7964	1·089	22·87	7·87	5·76	7·23
xi	—	Sudan, bred in cages from *solitaria*, H. B. Johnston ...									
xii	49 etc.	F_5 same as iv above, but hoppers isolated, each in its own cage	8	38·22	1·837	·8981	1·264	20·81	7·60	5·40	6·01

TABLE XI.

Locusta migratoria migratorioides, females: Averages and ratios of biometrical data. Measurements in mm., to 0·1 mm.

Series	L.d. number	Description	Number measured	A	A/F	M/T	H/T	F	H	M	T
i	568	Phase *solitaria* Vredendal, Van Rhyns Dorp, C.P., Dec. 1930-Jan. 1931	100	53·83	1·789	·8948	1·308	30·08	11·00	7·52	8·41
ii	41 etc.	F_1 crowded, in cages, from *solitaria*	28	47·18	1·955	·8509	1·147	24·13	8·49	6·30	7·40
iii	45 etc.	F_3 crowded, in cages, from *solitaria*	50	45·83	2·023	·8366	1·108	22·65	8·06	6·08	7·27
iv	49 etc.	F_5 crowded, in cages, from *solitaria*	50	44·64	2·037	·8306	1·093	21·91	7·65	5·81	7·00
v	564 / 566	F_5 black 1st instar selection, crowded, in cages, from *solitaria*	30	46·05	2·106	·8118	1·050	21·87	7·70	5·95	7·33
vi	572	Migrating swarms, Tanganyika, May 1931	20	52·58	2·124	·7699	·9914	24·76	8·64	6·71	8·72
vii	570	Migrating swarms, Tanganyika, March 1931	30	51·44	2·167	·7652	·9815	23·73	8·29	6·46	8·45
viii	572 / 570	Migrating swarms, Tanganyika, Nos. vi and vii combined ...	50	51·90	2·150	·7671	·9855	24·14	8·43	6·56	8·55
ix	—	Migrating swarms, Makoni, Southern Rhodesia 17.ix.1923	6	50·82	2·035	·8000	1·071	24·97	8·75	6·53	8·17
x	—	Migrating swarms, Sudan, 1930	4	53·05	2·118	·7886	1·000	25·05	8·75	6·90	8·75
xi	—	Sudan, bred in cages from *solitaria*, H. B. Johnston ...	5	48·20	1·790	·8346	1·131	26·92	9·16	6·76	8·10
xii	49 etc.	F_5 same as iv above, but hoppers isolated, each in its own cage	2	48·30	1·837	·9272	1·318	26·30	9·95	7·00	7·55

Taking the three ratios together, we find that the F_5 and F_5 black selection exceeded the Makoni series in *gregaria* characters in all three, while the F_3 went further than Makoni in the ratio A/F.

The material of series x was taken from migrating swarms in the Sudan. Comparing the ratios obtained, we find that this series is very close to series viii in M T and H T, being slightly lower in the former and higher in the latter. In the ratio A F the Sudan swarm specimens gave 2·059, distinctly smaller than that of the F_5 black selection series. In absolute size, the series x came very near series viii, as shown by the figures in column A.

Series xi, material bred in crowded cages from the phase *solitaria* by Mr. H. B. Johnston, came nearer to the extreme *gregaria* type than any other series in the ratio M T, and in H T it came second in this respect only to the F_5 black selection. But in A F series xi came nearest to *solitaria* with 1·874, while in A it gave an average of 42·86. In view of the small numbers measured in series ix, x and xi, the figures for these are not as dependable as those in the series where 30–100 specimens were available.

Table XI.—Females.

In this table we have the data for the females from the same sources as the males in the corresponding series of Table X. In the column A we note an interesting difference between *L. pardalina* and *L. m. migratorioides* in that the *solitaria* females of the latter exceed the *gregaria* females in size, whereas the reverse is true of *L. pardalina*. Arranging the series in descending order of size, we find the Tanganyika swarm specimens second, followed by Makoni, F_1, F_5 black selection, F_3 and F_5.

As for the ratio A F, there is a difference of 0·361 between the extreme *solitaria* and *gregaria* phases, which is somewhat greater than the corresponding difference in the male sex. The F_1 series comes nearer to *solitaria* than to *gregaria* with 1·955; the rest arranged in ascending order are F_3, Makoni, F_5 and F_5 black selection, and all these are nearer to *gregaria* than to *solitaria*.

In M/T, the difference between the *solitaria* and Tanganyika series is 0·1277, which is greater than that found in the male sex and also somewhat greater than the corresponding difference in females of *L. pardalina*. Here both F_1 and F_3 are nearer to *solitaria* than to *gregaria*, while the two F_5 lots and Makoni come closer to the extreme *gregaria*, the Makoni series going furthest in this direction.

Between the series i and viii there is a difference of 0·3225 in the ratio H/T, showing that the females differ more than the males in relative height of pronotum compared with the width of head. The F_1 series comes just about half way between the solitary and swarm phases with a ratio of 1·147. The F_3, F_5, Makoni and F_5 black selection series approach closer, in the order named, to the *gregaria* than to the *solitaria* type.

The series from swarms in the Sudan gave ratios approaching closely to those of the Tanganyika specimens. The cage-bred Sudan material came nearest the extreme solitary type in A/F; in M/T it was nearer *solitaria* than *gregaria*, with a ratio somewhat smaller than those of F_1 and F_3; in H/T it was slightly nearer to *gregaria*, falling between our F_1 and F_3.

Summary of Tables X and XI.

The main points of interest in the biometrical data on both sexes may be summarised as follows:—

(1) A strong divergence between the phases *solitaria* and *gregaria*, especially in the ratios A/F and H/T, but also wide enough in M/T so that the three ratios can be used in the classification of material.

(2) The material from Makoni, Southern Rhodesia, does not equal the extreme *gregaria* material from Tanganyika in biometrical proportions, but is much nearer to the latter than to extreme *solitaria* material; it should therefore be regarded as representing a proper swarm type and not an incipient swarm; this conclusion is supported by the Rhodesian records.

(3) The cage-bred crowded progeny of phase *solitaria* is nearer to *solitaria* than to *gregaria* in all cases in the F_1 generation; the F_3 generation is nearer *solitaria* in M/T, but nearer to *gregaria* in A/F and H/T; the unselected F_5 is nearer to *gregaria* in all ratios except M/T of the male sex, but goes further towards the extreme *gregaria* in this ratio than does the Makoni series; the F_5 selection of black first instar hoppers is very close to the Tanganyika series in all ratios, and is exceeded in this respect only in M/T of the females by the Makoni series.

(4) The cage-bred series approached very close to a regularly increasing variation towards the phase *gregaria* through the generations studied, except in A/F, where F_3 goes further than the unselected F_5 generation in the male sex.

We may therefore conclude that the progeny of the extreme *solitaria* material, when crowded together in cages, came so close in biometrical proportions to the extreme *gregaria* material from Tanganyika, that actual transformation of *solitaria* into *gregaria* took place in the cages. If the Makoni swarm material is used as the standard of comparison, the selected material of F_5 actually exceeded the specimens from this locality in *gregaria* characters in all ratios but one.

These conclusions are in accord with those reached in discussing the data in Table IX, where the coloration of the hoppers was the standard of comparison.

Bearing in mind the limitations of " swarm " life in cages, which were pointed out above at the end of the discussion on Tables IV and V (p. 315), and taking the experiments on *L. pardalina* and *L. m. migratorioides* together, the following conclusion is warranted :—

In the two species of locusts under discussion, the transformation of the phase *solitaria* into the phase *gregaria* was observed to take place in cages under crowded conditions. This conclusion is based on a study of the coloration of the hoppers and on biometrical measurements of the adults; the data are so convincing that the absolute specific identity of the two phases cannot be questioned, nor the fact that swarms of *gregaria* arise in nature from extreme *solitaria* parents without any admixture of pre-existing *gregaria* material.

Transformation of *gregaria* into *solitaria*.

The Coloration of the Hoppers.

The only living material of *L. m. migratorioides* available in Pretoria was the stock descended from the original 40 pairs of *solitaria* brought from the field early in 1929. Therefore it was not possible to carry out experiments parallel to those recorded in Tables IX, X and XI, in order to study the effects of isolation on progeny of the phase *gregaria* from the field. Failing field material of *gregaria*, the cage-crowded progeny of *solitaria* was used in isolation experiments.

After the hoppers in the crowded cages had acquired the coloration of the phase *gregaria* in the F_1 and F_2 generations, a number of individuals of the F_3, F_4 and F_5 generations were taken from the crowded cages and reared in isolation in cages of various kinds for different purposes. If taken for isolation in the first instar, the great majority of these hoppers would have been grey-mottled, *i.e.*, of *solitaria* type, for as stated above there was only a small percentage of black first instar hoppers

in some of the cages. *Gregaria* types could, however, be readily obtained in the second to the fifth instar.

About 30 of the first instar black hoppers were reared in isolation on growing grass and in various other cages ; without exception they all lost the *gregaria* coloration after one or two moults and became *solitaria* hoppers of a variety of colours. Some *gregaria* type hoppers were also isolated in the second instar and some in the third, and in all cases the *gregaria* characteristics were lost. An interesting feature was that the orange tended to disappear before the black in some cases (Pl. xviii, fig. 51).

The hoppers from crowded cages taken for isolation as grey individuals of the first instar cannot be cited as *gregaria* hoppers reared in isolation. They do, however, serve as controls on their fellows of the same parentage kept together in crowds. Of these hoppers that were grey in the first instar, about 200 were reared to the fourth or fifth instar in isolation, but in no case did the *gregaria* coloration appear on an isolated hopper.

We may therefore conclude that the experiments with this locust confirmed those undertaken with *L. pardalina* on a more extensive scale : whenever the hoppers were crowded they acquired the *gregaria* type of coloration, and as soon as they were reared in isolation the *gregaria* coloration either disappeared or failed to develop.

The Morphological Characters of the Adults.

A large proportion of the locusts reared in isolation, and referred to in the two preceding paragraphs, reached the adult stage and showed a very strong tendency to resemble the field *solitaria* material in the plastic characters of relative length of wing and shape of pronotum. Intermediate types also appeared, *i.e.*, all individuals reared in isolation did not have a conspicuously arched pronotum, but this is what one should expect in dealing with the variations of one and the same species.

In Tables X and XI there are included (series xii) 8 males and 2 females of the F_5 generation (not the black hopper selection) which were reared in isolation. If the series iv in these tables is regarded as having attained the characters of the phase *gregaria*, the data for series xii may be cited as proof of transformation in the opposite direction, from *gregaria* back to *solitaria*.

The 8 males of series xii in Table X were very small, as shown by the average wing-length of 38·22 mm. Their ratio A F was 1·837, coming closer to the *solitaria* average than that of any other series, and differing widely from 1·996, the ratio of the 67 males reared in a crowd. In M T the series xii gave 0·8981, the highest ratio in the whole table, while F_5 crowded gave 0·8217. The H T ratio was 1·264, closer to the *solitaria* than that of any other series.

The two females reared in isolation were much larger than the average for any of the crowded series. Their ratio A/F was 1·837, compared with 2·037 of the crowded F_5. In M/T they gave 0·9272, which is higher than the average for 100 *solitaria* females and very different from the ratio (0·8306) of their sisters reared in a crowd. In the ratio H/T, these two females also exceeded the average of the *solitaria* series.

The Effects of Crowding and Isolation upon the Progeny of Individual Pairs.

Tables XII and XIII.

Very striking differences in coloration as well as in morphological characters can be brought about in the progeny of one pair of adults by rearing some individuals in isolation and the rest under crowded conditions. A number of hoppers of the F_3 generation of *L. m. migratorioides* had been isolated in various types of cages, as stated in a preceding paragraph. When these became adults of the *solitaria* type, a number of males and females were paired and placed in cages with egg-tins. The

TABLE XII.

Locusta migratoria migratorioides, males: Parents and F_1 progeny of single pairs, isolated and crowded in cages. Averages and ratios of biometrical data. Measurements in mm., to 0·1 mm.

L.d. number	Description	Number measured	A	A/F	M/T	H/T	F	H	M	T
223	Progeny of pair L.d.223 reared in isolation	7	40·23	1·862	·8773	1·248	21·60	7·70	5·41	6·17
223	Progeny of pair L.d.223 crowded together	10	41·03	1·949	·8381	1·138	21·05	7·24	5·33	6·36
224	Progeny of pair L.d.224 reared in isolation	**3**	—	—	·9222	1·222	19·27	6·80	5·13	5·57
224	Progeny of pair L.d.224 crowded together	7	37·46	1·940	·8353	1·162	20·14	7·06	5·07	6·07
230	Parent, reared in isolation	1	40·4	1·669	·8750	1·281	24·2	8·2	5·6	6·4
230	Progeny reared in isolation	2	40·15	1·780	·8810	1·206	22·5	7·60	5·55	6·30
230	Progeny crowded together	8	42·18	1·934	·8296	1·127	21·81	7·52	5·54	6·68
330	Parent, reared in isolation	1	—	—	·8572	1·214	19·4	6·8	4·8	5·6
330	Progeny reared in isolation	3	35·13	1·824	·9325	1·233	19·27	6·70	5·07	5·43
330	Progeny crowded together	6	38·18	2·017	·8617	1·150	18·93	6·65	4·98	5·78

TABLE XIII.

Locusta migratoria migratorioides, females: F_1 progeny of single pairs, isolated and crowded in cages. Averages and ratios of biometrical data. Measurements in mm., to 0·1 mm.

L.d. number	Description	Number measured	A	A/F	M/T	H/T	F	H	M	T
223	Progeny of pair L.d.223 reared in isolation	8	51·90	1·920	·8729	1·263	27·02	10·31	7·12	8·16
223	Progeny of pair L.d.223 crowded together	10	46·34	1·997	·8471	1·157	23·20	8·40	6·15	7·26
224	Progeny of pair L.d.224 reared in isolation	3	42·87	1·845	·8679	1·255	23·23	8·87	6·13	7·07
224	Progeny of pair L.d.224 crowded together	7	44·08	1·940	·8446	1·139	22·71	8·17	6·06	7·17
230	Progeny of pair L.d.230 reared in isolation	1	45·0	1·837	·9028	1·194	24·5	8·6	6·5	7·2
230	Progeny of pair L.d.230 crowded together	4	48·30	1·994	·8333	1·096	24·22	8·55	6·50	7·80
330	Progeny of pair L.d.330 reared in isolation	2	40·70	1·813	·9380	1·295	22·45	8·35	6·05	6·45
330	Progeny of pair L.d.330 crowded together	3	41·90	2·008	·8528	1·142	20·87	7·50	5·60	6·57

progeny obtained from these pairs were divided into two lots: some were reared in isolation and the rest in a crowd, each crowd consisting of the progeny of one pair only. The effects of this treatment on the coloration of the hoppers was that those in isolation invariably showed different types of *solitaria* coloration, while a large majority of the crowded hoppers developed the *gregaria* coloration from the second or third instar onwards.

When this progeny of the single pair had reached the adult stage, striking differences were noticeable between the isolated and crowded individuals in the relative length of the wings and the shape of the pronotum. Some small series of these adults were measured in the same way as those whose measurements are recorded in Tables X and XI; the results, which are tabulated in Tables XII and XIII, show the wide variations obtainable from one pair of parents during the course of one nymphal development lasting about eight weeks.

Table XII gives the averages and ratios obtained from the measurements of the male progeny of four pairs, grouped together under the L.d. record numbers of each pair. In two cases the male parents were also available, and their measurements are added. The corresponding female progeny is listed under the same numbers in Table XIII.

It is a striking fact that the trend of the variation in each of the double groups of isolated and crowded progeny is distinctly in the direction of the *solitaria* and *gregaria* characters, respectively. This is true of both sexes and in all three ratios. The differences are not as large as those between the extreme *solitaria* and *gregaria* series in Tables X and XI, but one would not expect such a great divergence after a few weeks in the progeny of the same parents. Nevertheless, the differences are remarkably large in several cases.

Without going into great detail, a few of the interesting cases may be briefly compared with the figures in Tables X and XI. In Table XII, we note that the crowded progeny of No. 223 in the ratio M/T gives 0·8381, a ratio that is quite close to that for the Makoni series in Table X, 0·8346; the isolated progeny of No. 223 has this ratio 0·8773. In H/T, No. 223, crowded, gives 1·138, which is nearer to the extreme swarm figure, 1·002, than to the extreme solitary ratio 1·305.

The crowded series of No. 230 shows a ratio 0·8296 in M/T, which comes nearer to the ratio of extreme *gregaria*, 0·7584, than do those of the Makoni series or the F_3 generation of Table X. In H/T, No. 230 has 1·127, which is nearer to *gregaria* than to *solitaria*, and also goes further in the direction of *gregaria* than the F_3 generation.

The progeny of No. 330, crowded, has in A/F a ratio 2·017, and the isolated series has 1·824; the ratio 2·017 is much nearer to *gregaria* than to *solitaria*, and surpasses those of the Makoni, F_5 and F_3 series of Table X in this respect.

Coming to the females in Table XIII, we find that No. 230, crowded, has the ratio H/T 1·096; this is nearer to *gregaria*, and goes further in this direction than the ratio for F_3 in Table XI. The crowded progeny of No. 330 has the ratio A/F 2·008, which is nearer *gregaria* than *solitaria*, and distinctly higher than that of the isolated progeny of the same parents.

Resemblance to the colour of the environment.

Experiments in Painted Cages.

The experiments with painted boxes and painted gauze cylinders, described in the section on *L. pardalina*, were duplicated on approximately the same scale with hoppers of *L. m. migratorioides*, and the results were almost identical in the two species.

For the type of cage used, the treatment of the hoppers, and the method of arriving at the results, the reader is referred to the corresponding parts of the section on *L. pardalina* (p. 321).

The material used was taken from the crowded progeny of the 40 pairs of adults of the phase *solitaria* from the field. The majority of the hoppers were placed in the painted cages in their first instar, and all of them were of the grey type characteristic of the phase *solitaria*; other hoppers used were in their second to fourth instars, and of various colour types.

In view of the fact that the painted boxes and cylinders gave the same results, these two types of cages will be treated together in discussing results obtained with this species. Both boxes and cylinders were used for white, black, grey, yellow and brown.

On Pl. xviii, figs. 45–50 represent locusts which developed resemblance to the backgrounds in these experiments. In four of these figures the adults are represented; the hoppers of the fifth instar showed more striking resemblance, especially in Nos. 45 and 46, but unfortunately the artist was unable to paint these specimens before they became adults.

White.

Twenty hoppers were confined in white cages and afterwards classified according to the degree of resemblance as follows: good 9, fair 9, and slight 2; none were without any resemblance to the background, and only two showed a slight degree of resemblance. Eleven were grey hoppers of the first instar when put in: 5 showed good resemblance, one in the second, two in the third and two in the fifth instar; 5 were classed as having fair resemblance, one in the third, one in the fourth and three in the fifth instar; one hopper showed slight resemblance to white in the fifth. One was a second instar *transiens* type which was described as good in the fourth. Two *gregaria* hoppers of the third instar placed on white were described as showing good and fair resemblance in the fifth instar. Five others in the third instar were used, one of which deserves special mention: it had become black in a black box and was transferred to white; after 19 days, in its fifth instar, it was described as "dull yellow with minute black specks" and classed as showing good resemblance. One fourth instar black hopper, from a black box, became light grey in the fifth instar on white, and was noted as a case of fair resemblance.

Black.

On this colour 15 hoppers were tested, with the following result: no resemblance 1, slight 1, fair 2, and good 11. Ten were put in as grey first instar hoppers: 7 were noted as having good resemblance, 1 in the second instar, 1 in the third, 2 in the fourth and 3 in the fifth; 1 had fair resemblance in the third, 1 slight in the second and the tenth developed no black colour at all. The remaining 5 hoppers were in the second and third instars when put on black, but only one should be specially mentioned: a second instar hopper transferred from a white cage and described as dirty white; in the third it was noted as grey-white, and in the fourth instar, 27 days after the transfer, it had become practically pitch black in colour.

The hoppers of *L. m. migratorioides* were exceedingly sensitive to the influence of the black background, and some of the cases in which good resemblance was noted were remarkable, the insects being deep sooty black everywhere except on the antennae. It was literally very difficult to see the hopper on its black background in many cases. On white, grey and yellow, some of the insects also showed striking imitations of the background colour, but they did not look as unreal and unheard of as the pitch black ones.

PLATE XVIII.

LOCUSTA MIGRATORIA MIGRATORIOIDES (RCH. & FRM.).

Figures 45-50: locusts reared in painted boxes.

Figure

45 ph. *solitaria* ♀ adult, reared in box painted black, L.d. 325, 17 ii. 1931. (× 1·5)

46 ph. *solitaria* ♀ adult, reared in box painted white, L.d. 318, 26 x. 1930. (× 1·5)

47 ph. *solitaria* ♂ adult, reared in box painted light brown under brown glass, L.d. 263, 18 x. 1930. (× 1·5)

48 ph. *solitaria* ♂ 5th instar, reared in box painted in black and white stripes about 1/12″ wide, L.d. 262, 28 vi. 1930. (× 1·5)

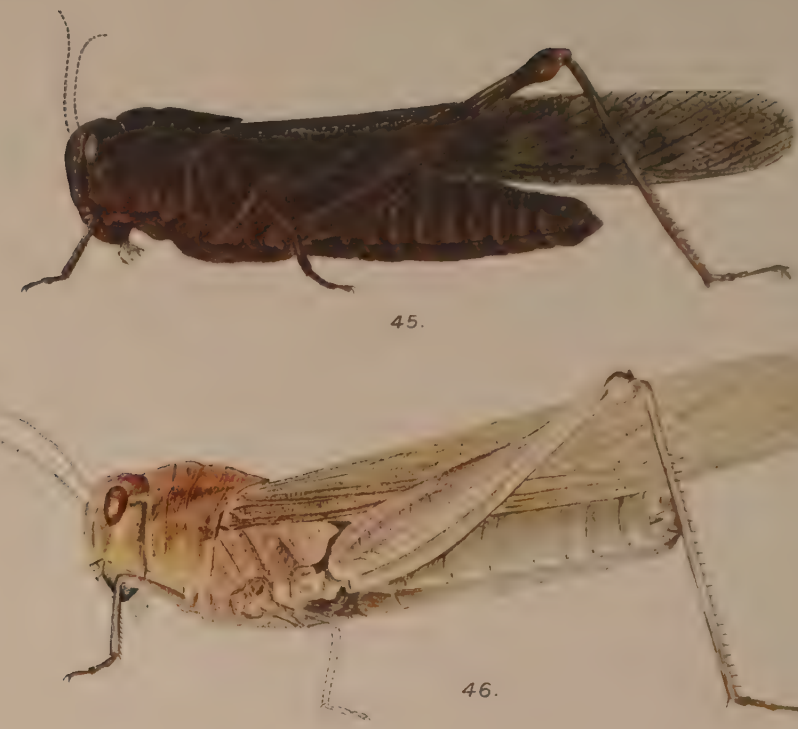
49 ph. *solitaria* ♂ 5th instar, reared in box painted aniline yellow,* L.d. 218, 16 vii. 1930. (× 1·5)

50 ph. *solitaria* ♂ adult, reared in box painted squill blue,* under blue glass, L.d. 216, 18 x. 30. (× 1·5)

51 ph. *transiens* ♂ 4th instar, placed in celluloid cylinder over growing barley as 2nd instar swarm type on 25 iii, 1931; killed and painted 10 v. 1931, L.d. 45/57. (× 1·5)

52 ph. *gregaria* ♀ 4th instar, from cage, 18″×9″×15″, containing about 100 hoppers, L.d. 315, 10 ii. 1931. (× 1·5)

* Colours according to Ridgway.



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Deep Mouse Grey.

Seven hoppers were kept in grey cages; three were put in as grey first instar hoppers, and all were described as good imitations, two in their third and one in its fifth instar. One was a grey second instar, and it developed a type of grey very close to that of the cage in the third. One was a blackish-brown third, which became a good grey in the fifth. Two *gregaria* type hoppers of the third instar were also tested: in the fifth both were grey, one noted as having good and the other as fair resemblance to the cage. Of the seven put on grey, only one was classed as a case of fair imitation, and six as good.

Aniline Yellow and Bay Brown.

On yellow we tested five hoppers; four resembled the cage very closely and were noted as good, and the fifth showed only fair resemblance. Four were in the first instar, grey; three were noted as good, two in the third and one in the fifth; the fourth showed fair resemblance in its fourth instar. One *gregaria* hopper put in as a third became a good yellow type in the fifth.

In cages painted bay brown, three hoppers were confined, and all three developed good imitation colours. Two were first instar grey when put in; one was brown in the second, the other in the fifth. A third instar *gregaria* hopper became chocolate brown in its fifth instar, after 47 days.

Summary of the experiments on colours which gave positive results.

Table XIV.

As in the case of *L. pardalina*, the use of cages painted white, black, grey, yellow and brown resulted in distinct imitations of the background in a large majority of the hoppers. The cases of good and fair resemblance together totalled 92 per cent., leaving only 8 per cent. in which the result was no imitation or slight imitation. These results therefore confirmed those obtained with *L. pardalina*, and support the conclusions reached above in this connection.

TABLE XIV.

The data obtained for the colours which gave positive results.

Colour of background	Type of cage	Hoppers, classified according to degree of resemblance to the background				Total hoppers
		None	Slight	Fair	Good	
White	Box	–	1	5	7	13
	Cylinder	–	1	4	2	7
Black	Box	–	–	1	6	7
	Cylinder	1	1	1	5	8
Deep mouse grey ...	Box	–	–	1	5	6
	Cylinder	–	–	–	1	1
Aniline yellow ...	Box	–	–	–	4	4
	Cylinder	–	–	1	–	1
Bay (brown)	Box	–	–	–	3	3
Totals		1	3	13	33	50
Percentages ...		2	6	26	66	—

Experiments with colours on which the results were largely negative.

In gauze cylinders painted grass green, 7 grey hoppers of the first instar lived long enough to undergo two or more moults. No trace of green was seen on any of them;

one lived to the third, one to the fourth and five to the fifth instar on the green for periods varying from 42 to 116 days.

On eosine pink two hoppers put in as grey in the first instar lived to the fifth without developing any trace of pink. Two hoppers were also tested on pale blue backgrounds resembling the squill blue and dusky greenish blue of Ridgway; one lived to the third and the other to the fifth without showing any blue.

Combinations of two colours were also tried on a small scale, with inconclusive results. In boxes with alternating black and white lines about $\frac{1}{12}$ inch wide, three hoppers of the first instar were tested; one was yellow-brown in the fifth and had no stripes after 72 days; the second was described in the third as "dirty white with darker lines on the pronotum; slight resemblance to striped box"; the third became black with silvery grey spots and lines from the third to the fifth instar, showing a striking resemblance to the box (Pl. xviii, fig. 48).

Broader black and white bands, about $\frac{1}{6}$ inch wide, were also tried. One first instar grey hopper remained grey to the fifth instar in this box, and showed no tendency to develop a banded coloration after 53 days. A third instar *gregaria* type hopper showed a slight degree of resemblance in the fifth instar, after 69 days, being described as "grey with lighter grey stripes on the pronotum." Another third instar hopper of the *transiens* type showed no striped appearance in the fifth after 34 days.

Grey and yellow were also tested, both narrow and broader stripes being used, as in black and white. Two hoppers reared in these from the first to the fifth instar both showed good resemblance to yellow, and one also had a little grey, but there was no striped appearance.

It should be pointed out that the hoppers of *L. m. migratorioides* often bear longitudinal stripes of a paler colour on the dorso-lateral aspect of the head and prothorax, as is shown on figures 36, 37, 49, 51 and 62. For this reason the longitudinal stripes on the pronotum of the hopper, represented by figure 48, should perhaps not be regarded too confidently as an imitation of the striped box. But, on the other hand, similar pale stripes were not seen on black hoppers reared in black boxes (fig. 45), and the figure 48 shows a distinctly banded coloration on the hind femur and also on certain other parts of the body.

In boxes imitating the *gregaria* type of hopper coloration, *i.e.*, orange rufous and black, one hopper showed good imitation of the black only, and a second had neither black nor orange.

Summarising the results obtained with this group of colours, we may conclude that green and pink backgrounds had no effect on the coloration of the hoppers; this agrees with the results obtained with *L. pardalina*.

The combinations of two colours were tried on a small scale only: one very striking resemblance to black and white appeared in a striped box (fig. 48), suggesting interesting possibilities in this direction. It does not seem probable the hoppers will be found to imitate a background painted orange.

Experiments with coloured Glass.

Four kinds of coloured window glass were used as lids in wooden boxes, like those used for the painted background experiments (Pl. xxxviii, fig. 198), in order to test the effect of coloured light on the coloration of the hoppers. Dr. V. Voss kindly tested samples of the glass, and reported that the following spectral ranges were transmitted: blue glass: 4,000–4,800 A-U, and also a green strip 5,500–5,650 and a red strip 6,900–7,100; green 5,000–6,100; brown 5,200–6,800; and red 6,000–6,900. The light transmitted by these samples of coloured glass was therefore by no means spectrally pure in the case of blue, green, or red, and the brown glass had a range which included green, yellow, orange and red.

At first the coloured glass was placed in unpainted teak boxes, and one hopper was reared under each. No resemblance to the colour of the glass resulted. In another series of eight tests, three to five hoppers were reared together in unpainted boxes under the four kinds of glass ; in most cases three hoppers survived in a cage, and these tended to develop *transiens* and *gregaria* coloration. Under green glass two hoppers together in one cage showed good resemblance to the brown colour of the unpainted teak, but no green coloration.

Then we tried the coloured glass over boxes painted in corresponding colours. The brown glass was placed over a box painted with a light coat of bay brown : four hoppers reared in isolation in this showed resemblance to brown, two being classed as good and two as fair (Pl. xviii, fig. 47). The blue glass was used over a pale blue box (squill blue of Ridgway) : one hopper reared to the fifth showed no blue ; another was noted in the fourth instar, after 63 days, as "grey with distinct bluish tinge" and considered as one showing fair resemblance ; a third reared from the first instar to the adult stage had a distinct blue colour on parts of the body (Pl. xviii, fig. 50).

The green glass was placed over one box painted dark green (antique) and another grass green : one hopper was reared in each cage, but neither developed a trace of green. In all these tests of coloured glass, the insects were fed in the usual way, bits of green food being dropped into the cages twice a day.

On the whole, the results obtained with coloured glass in the case of both species of locusts were inconclusive, because only a small number of hoppers were reared under each kind of glass. Under blue glass over a pale blue background, there was a distinct tendency to produce blue in two hoppers out of four. Under brown glass over a brown background, four hoppers out of five showed a distinct resemblance to brown, but brown under plain glass was one of the backgrounds on which all hoppers developed a distinctly brown coloration, therefore it is very doubtful whether the brown glass had any effect.

Blinded Hoppers in painted Boxes.

In order to determine whether the eyes are concerned in the processes involved in the imitation of colours, attempts were made to cover the eyes of hoppers of *L. m. migratorioides* while they were being reared in painted boxes. Opaque, quickly-drying substances were painted over the compound eyes and ocelli at intervals of about a week, and after every moult. When the hoppers were examined, notes were taken on the extent to which the eyes were covered, and whenever necessary more paint was added in order to make the blinding as complete as possible. All the exuviae were not recovered for examination, some being eaten by the insects, but the majority were found and examined against the light under a hand lens. In the following records of the experiments, three degrees of blinding are noted : complete, fair and slight. This grading refers to the whole period during which the experiment lasted, and represents a summary of the notes on the thoroughness with which the eyes were covered, but it cannot be claimed to be more than an approximation. It is not practicable to paint the eyes immediately after the moult, and one could not watch the insect all day to see it moulting, therefore all hoppers had their eyes uncovered for some hours after moults.

In most cases a suspension of lamp-black in a solution of shellac in 95 per cent. alcohol was used. This stuck to the cuticula quite well in hoppers living a quiet life in isolation, but was very quickly lost by those living in a small crowd, owing to the continual jumping and the impact against the cage. In the experiments discussed here, only one hopper was kept in each cage. We also tried a quickly-drying copper enamel paint, but found the shellac more satisfactory.

Two hoppers were noted as having been completely blinded during the period spent in the colour boxes. The first was a second instar hopper, blackish brown in

colour, placed in a box painted white ; after 46 days it was described in the fourth instar as grey-yellowish white and showing good resemblance to the background.

The second hopper was put as first instar grey into a pale blue (squill) box under blue glass ; in the fourth and fifth instars it was noted after 59 and 77 days respectively as " bluish grey—good resemblance."

In five cases the blinding was considered to have been fair only : for periods of several days the hopper had parts of its eyes uncovered, although it was more or less completely blinded for many other periods of several days or weeks. Three of these five hoppers showed good resemblance after two to four moults on white, yellow and bay brown plus brown glass ; the two others had fair resemblance only after one to three moults on grey and yellow backgrounds. One of these cases deserves special mention : a third instar hopper had become pitch black in a black box, unblinded ; it was transferred to a yellow box and blinded, and in the fifth instar it was noted as " greyish yellow—good resemblance."

Finally, two hoppers were described as having had only a slight degree of blinding. They were both reared from first grey to fifth instar ; one showed good resemblance on black, the other fair resemblance on grey.

Taking into consideration only the seven cases in which the blinding was described as complete and fair, these gave five cases of good imitation of the background and two of fair imitation. These results indicate that the organs of vision are probably not involved in the imitation of the coloration of the background.

The Problem of the Green Hopper.

I have not had much opportunity of studying the hoppers of *L. m. migratorioides* in the field, but I believe a large percentage will be found to be green. As stated above, out of 415 adults taken in lucerne fields, about 56 per cent. were green, and this means that they were in all probability green during the hopper stages. In the breeding cages green hoppers were very rarely seen except in the celluloid cages in which they had abundant green food in a moist atmosphere.

With this species I carried out a series of experiments on the green colour in the same types of cages and under the same conditions as those described above for *L. pardalina*. In this case it will therefore not be necessary to describe the cages or the treatment, but the results will be briefly discussed and compared with those obtained in the other species.

Gauze Cylinders over Growing Food.

In the short gauze cylinders 9 grey hoppers were placed in their first instar ; 6 became green in 7 to 33 days, two in the second, three in the third and one in the fourth instar ; the other three hoppers remained grey. The percentage which became green was higher in this species than in *L. pardalina*.

In the tall gauze cylinders four hoppers were tested ; they were put in as second instar grey, and all became green, one in the fourth and three in the third instar, in periods varying from 19 to 32 days. This indicates that the hoppers of *L. m. migratorioides* become green more readily than those of *L. pardalina* under the conditions obtaining in these cages, since in the latter species no green appeared on 8 hoppers tested.

Table XV.

Celluloid Cylinders over Growing Food.

The results of the experiments in celluloid cylinders over growing grass or barley are summarised in Table XV. The 82 hoppers which became green were not all of

the same shade of green ; they were classified as bright green 64, fair green 12 and poor green 6. The percentage of green obtained, 86·3, was higher than in the case of *L. pardalina*, where the figure was 72·9 (Table VII, p. 329).

The minimum number of days required to become green was 3 days ; a brown hopper put on grass in its fourth instar was noted as a poor type of green three days later, in the fifth instar. Two yellow hoppers placed on grass became bright green in 4 days, and several others acquired the green in 7 and 8 days. In all cases the green only became distinctly visible after one or more moults had occurred.

TABLE XV.

L. m. migratorioides : Hoppers reared in celluloid over growing food.

Instar and colour when placed on growing food	Became green in instar				Total	Average number of days required to become green	Remained grey	Total green and grey
	2	3	4	5				
1st *gregaria*	1	7	–	2	10	26·8	2	12
1st *transiens*	1	3	–	–	4	20·3	–	4
1st grey	15	13	10	2	40	17	6	46
2nd *gregaria*	–	4	8	3	15	37·8	5	20
2nd grey	–	2	–	–	2	10	–	2
2nd brown	–	1	1	–	2	9	–	2
3rd grey	–	–	1	1	2	18	–	2
3rd brown	–	–	1	–	1	—	–	1
4th grey	–	–	–	2	2	7·5	–	2
4th yellow	–	–	–	1	1	4	–	1
4th brown	–	–	–	3	3	14·5	–	3
Totals					82		13	95
Percentages					86·3		13·7	—

The Progeny of Green and Non-green Parents.

The F_1 progeny of a pair of green adults of *L. m. migratorioides* were tested for ability to become green in celluloid over growing green food ; 34 hoppers were used, but 52 experiments were undertaken : after a hopper had developed a good green colour, it would be transferred to another cage with different conditions, and then after it had lost its green it would be returned to growing grass and counted as if it had been a different insect.

All the hoppers were grey in their first instar when put on grass the first time, and 33 out of 34 became green in an average period of 14·9 days. Eleven were placed on grass in their third instar as grey or grey-black, and of these 10 became green in an average period of 14 days. Seven were grey when placed on grass in their fourth instar, and of this number six became green in an average of 16·7 days. We see, therefore, that only three tests out of 52 gave a negative result : one hopper remained grey on grass for 30 days from the first to the third instar and died in the third ; the two others had been green once before in the second and third instars, but failed to acquire green again after one and two moults respectively when replaced on grass. If all the progeny of this " green by green " pair had been left on grass throughout

their development as hoppers, a result of 100 per cent. green may possibly have been obtained. Counting 52 green and 3 non-green, we arrive at the percentages 94·2 green and 5·8 non-green.

The progeny of a green male mated with a non-green female was also tested in celluloid over grass. Both parents had been reared throughout their developmental instars in celluloid over grass: the male became green, but the female remained grey. Twenty-eight insects lived long enough to undergo one or more moults, and of these 19 became green, or 67·9 per cent., and 9 remained grey, or 32·1 per cent. The average period required to acquire green was 29·8 days.

Comparing these results from hoppers of known parentage with those obtained in similar tests with *L. pardalina*, we note that green × green gave a higher percentage of green progeny in *L. m. migratorioides*. This supports the view expressed above that the latter acquires green in its immature stages more readily than the former. The case of green male × non-green female gave 67·9 per cent. green, as against 86·3 per cent. in miscellaneous hoppers and 94·2 per cent. in green × green, indicating that in this species as well as in *L. pardalina*, hereditary factors may possibly be concerned in determining whether a particular individual possesses the ability to acquire green under suitable conditions.

A constant Supply of Green Food in a moist Atmosphere.

In the case of *L. pardalina*, hoppers confined in grey wire gauze cages were supplied with blades of grass standing in water, to see whether green would develop, but the result was negative. A similar experiment was undertaken with *L. m. migratorioides*, but in this case the hoppers were kept in celluloid cylinders on sand, and the sand as well as the calico covers were watered several times a day. Six grey hoppers were confined in these cages from their first instar; two lived to the fourth and four to the fifth, but not a trace of green developed in them. The number tested was small, but in view of the fact that about 86 per cent. of the hoppers became green in celluloid over growing food, it seems improbable that all of these six hoppers should have lacked the ability to acquire green.

This result is puzzling; although the degree of moisture in the cages was not measured, there is no doubt that a relatively high degree of humidity must have been present most of the time, although the cages over growing grass would undoubtedly have been more moist. The food supply was more or less constant, but certainly not as constant as in cages with growing food, and this may be the reason for the failure to develop green. In support of this hypothesis the case of tall gauze cylinders over growing food may be cited; in these cages four hoppers of *L. m. migratorioides* were tested, and all became green.

The Fate of the Green under altered Conditions.

The experiments discussed under this heading in the section on *L. pardalina* were repeated and extended in certain directions with hoppers of *L. m. migratorioides*. The cages, methods of feeding and other treatment were the same for both species, except where the contrary is stated. The hoppers were taken from the celluloid cylinders and wire cages in which they had acquired the green colour.

Wire Gauze Cylinders on Boards.

One hopper showing poor green in the second instar was tested, it became yellowish brown and lost all green in 7 days after one moult. Three bright green individuals in the third instar were transferred to these cages; in the fourth one showed a trace of

green only and the other two had no green at all. Three hoppers, bright green in the fourth instar, were used ; one was noted as fairly green in the fifth after 14 days and then it died ; the other two had no green at all in the fifth instar after 12 and 18 days respectively.

Altogether 7 hoppers were placed in these cages : 5 lost all the green, one retained a trace only, and one remained green.

Green Backgrounds.

A bright green hopper in its third instar was placed in a box painted grass green and covered with a piece of green window glass : after 21 days it was described in the fifth instar as " light brown, no green."

Four bright green hoppers were placed in boxes lined with mirrors and covered with a piece of green photographic celluloid held in place between two pieces of glass. This green material transmitted a spectral range of 4,700 A-U—5,750, plus a short red strip 6,800-7,050. It was used instead of the green glass in case it might have a different effect on the hoppers, and the mirrors were used to have the same kind of light reflected from all sides. The insects were fed twice a day only.

Three of the hoppers were in the third instar ; they were all described as having no green colour in the fourth instar. The fourth was in the fourth instar, when put in the mirror box ; in the fifth it had only a very faint trace of green.

Two green hoppers were also placed in wire gauze cylinders painted grass green, and fed by means of blades of grass kept in bottles of water. One was in the second, fair green, when the experiment began ; in the second after 6 days it was only faintly green and in the third it had no green colour at all. The other was put in as third instar bright green ; after 6 days it was still bright green in the fourth instar, and 20 days later it had become dull blackish green.

Of the 7 hoppers placed on green backgrounds, 5 lost all green completely, one retained a trace only, and the seventh became dull blackish green. Evidently the green colour of the environment had no influence on the processes involved in the retention or loss of the green colour.

Cages painted in various Colours.

Two green hoppers were confined in black gauze cylinders and fed twice a day only : a bright green third instar hopper was noted as dull greyish green in its fifth instar after 30 days. The second hopper was bright green in the fourth instar at the start, and after 7 days it was noted as a fifth, " yellowish brown, no green."

Two bright green hoppers of the fourth instar were confined in gauze cylinders painted Nopal red, and fed by means of blades of grass kept in bottles of water ; in the fifth instar one had lost all its green and the other was grey with a trace of green only.

Grey galvanized (unpainted) gauze cylinders were also used in conjunction with feeding on blades of grass standing in water. A bright green hopper placed in one of these cages in its second instar was noted as being very dark grey with only a trace of green in the third after 10 days. Another hopper was in the third instar, also bright green, and after 10 days it had become yellowish brown and showed only a trace of green.

Summing up, we find that 6 bright green hoppers were placed in black, red and grey cages : 2 lost all their green, 3 retained a trace only, and one became dull greyish green.

A moist Atmosphere.

Twelve green hoppers were placed in celluloid cylinders on moist sand and fed on blades of grass kept in water; nine definitely lost their green colour, one remained about as green as it was, and two which were only slightly green at the start became bright green after two moults. The loss of green in 9 cases out of 12 is difficult to understand in view of the fact that six hoppers of *L. pardalina* placed in similar cages on the same table at about the same time all retained the green. The degree of moisture in the atmosphere of these cages was not definitely regulated and the conditions in adjoining cages would no doubt have shown considerable variations if they could have been studied minutely. Nevertheless it is interesting that such a distinct divergence between the two species should have occurred in these cages. The numbers tested were small, therefore definite conclusions are not warranted.

Three other green hoppers of *L. migratorioides* were placed in celluloid cages in which the atmosphere was undoubtedly more nearly saturated than in those standing in moist soil. Here the cage was a cylinder of celluloid with a cover and floor of the same material and a small sliding door of celluloid in the cover. The floor was perforated, and the walls projected below it, forming a lower compartment in which a jar of water was kept. Standing in the sun, these cages nearly always showed considerable condensation of water on the walls. The feeding was provided for by means of blades of grass standing in water and pushed into the cage through a small slit in the side as required. Two of these green hoppers retained their green after two moults, but the third did not remain green.

A dry Atmosphere.

Eight bright green hoppers were placed in celluloid on dry sand and fed on blades of grass kept in water. Seven lost the green completely, two after two moults and five after one moult; the eighth was still faintly green in the adult stage after 33 days. In this species the green is retained by the adults for a much longer period than in *L. pardalina*.

Food devoid of Chlorophyll.

Green hoppers were also confined in cages on foods which contained no chlorophyll; in all cases the atmosphere in the cages was very moist. On the flowers of a bright red variety of *Canna indica* the insects were confined in celluloid cylinders in such a way that they were forced to remain on the petals; the flowers stood in bottles of water and were changed about once a week. Fourteen green hoppers were kept on these flowers: 10 definitely lost their green colour after one or two moults, and 4 retained the green through two to four instars. One of the hoppers which remained green was described in the fourth and fifth instars as "bright green, non-green parts reddish-brown," but there was no other case of imitation of the red colour; although a general tendency to take on a very dark coloration was strongly in evidence.

The yellow flowers of *Coreopsis* were used in the same way as those of *Canna indica* as food for two bright green hoppers: one, in the second instar, became pale yellowish green after 10 days and died in the moult; the other moulted from the third to the fourth instar and remained green until it died, 14 days after the beginning of the experiment.

On the yellow leaves of *Ligustrum vulgare* one bright green hopper lived for six days only.

Beetroots (*Beta vulgaris*), with the tops cut off, were gouged out and roughened and placed under celluloid cylinders in such a way that they formed the floors of the cages. Five green hoppers were placed in these cages with no other food;

two died after 5 and 7 days without moulting ; one lost the green colour in about 8 days and died before moulting ; one was a second instar bright green hopper, and in the third it was described as pale grey ; the fifth hopper moulted once and retained some of its green colour.

Two green hoppers of the third instar were placed in celluloid over growing beetroot seedlings about 2 inches in height : one moulted to the fourth but died after 5 days after it had turned pale green ; the other lived for 3 days only.

Reviewing the results on food which contained no chlorophyll, we find (1) that it was difficult to keep the insects alive on the foods used, and (2) that there was a distinct tendency to lose the green colour under these conditions, although the hoppers were kept in a moist atmosphere.

Miscellaneous Experiments.

Certain indications concerning the influence of light on the green coloration are provided by the following experiments. A second instar hopper showing poor green coloration was placed in a celluloid cylinder over growing grass, and the cage was covered with a tin can admitting no light. The insect survived for 34 days under these conditions : in the third it was bright green and in the fourth instar bright green at first, but later it became yellowish green.

A wooden box painted black on the inside and white on the outside was provided with ventilators which admitted air but no light. Under this box a number of hoppers were placed in celluloid cylinders over growing grass. One of the grey first instar hoppers which were confined under these conditions became bright green in the second instar after about 10 days.

The bottom was knocked out of a brown bottle so that it could be pressed into the soil of a box of growing grass, and a bright green hopper of the second instar was confined under it. In the fourth instar this insect was still bright green, and in the fifth it became greyish green, but there was no longer an abundance of green grass towards the end of the experiment. The glass of this bottle was tested spectroscopically and found to transmit 5,100-6,900 A-U.

These three tests suggest that the green colour can develop in the absence of light if an abundance of succulent green food is provided in a moist atmosphere.

In view of the fact that the grey colour of galvanized wire gauze was readily acquired by hoppers reared in cages made of this material, we tested its influence on green hoppers in celluloid cylinders. Three bright green hoppers were confined in wire gauze cages, about 7 inches high and 2 inches in diameter, standing on growing grass, and these were enclosed in celluloid cylinders covered with cloth or mosquito netting ; all three hoppers retained their green colour for 23 to 50 days through two or three instars. Here the moist atmosphere and abundance of green food were present, and in addition a partial background of a colour readily imitated. The result confirms those obtained with this species in tall wire gauze cylinders in which 4 out of 4 hoppers became green.

General Conclusions on the Green Colour.

The results obtained with *L. m. migratorioides* confirmed the conclusions arrived at under this heading in the section on *L. pardalina* in all respects except one. The

former gave evidence of being able to acquire the green colour more readily than the latter, as is shown by the following figures :—

Percentage of hoppers which became green on growing food.

	L.m.m.	*L.p.*
In short gauze cylinders	$66\frac{2}{3}$	48
In tall gauze cylinders	100	0
In celluloid cylinders	86·3	72·9

In view of this, it was very surprising to find that 6 hoppers of *L. pardalina* retained the green in celluloid cages on wet sand, in which they were fed on blades of grass standing in water, whereas 9 out of 12 hoppers of *L. m. migratorioides* lost their green in these cages.

On the food devoid of chlorophyll, a larger number of hoppers of *L. m. migratorioides* were reared than was the case in the other species, but the results were the same.

A point of interest brought out by the experiments on *L. m. migratorioides* is that the green colour can apparently develop in complete darkness.

The only conditions under which a majority of green hoppers of *L. m. migratorioides* retained their green was in a saturated atmosphere, two out of three remaining green.

Reviewing all the tests carried out with green hoppers of *L. m. migratorioides*, one feels convinced that the preliminary conclusions arrived at above on the nature of the green in *L. pardalina* are equally applicable to this species.

Plotnikov (1927) reported that hoppers of *L. migratoria* bred by him in isolation in glass containers always acquired a green colour, and stated that water condensed on the walls of the jars. It is obvious that he gave these hoppers the two conditions—moist atmosphere and succulent food—which the writer has found essential for the production of green in *L. pardalina* and *L. m. migratorioides*.

Several changes in coloration during the development of one hopper.

Table XVI.

Table XVI records the changes in coloration observed in 15 different hoppers, each of which changed colour three times, and gives the details about the conditions which caused these changes. In addition to these 15 hoppers, at least a dozen other cases could be cited from the breeding records of hoppers which changed colour twice, *e.g.*, from grey to black and then from black to green. Two of these cases deserve special notice :—

No. L.d. 324 was put in a box painted black when it was a grey hopper of the first instar. In the third it was described as deep sooty black and transferred to a box painted white, and 7 days after the transfer it was noted in the fourth instar as dark bluish grey. In the fifth instar it became greyish yellow, very pale compared with its colour in the third instar, and was noted as showing a good resemblance to white.

No. L.d. 325 was a first instar grey hopper that became greyish white in a white box and was transferred in its third instar to a black box. In the fifth instar it was noted as pitch black, 19 days after the transfer.

TABLE XVI.

Hoppers of *Locusta migratoria migratorioides* which changed colour three times as a result of altered conditions of the environment.

L.d.	1st instar	2nd instar		3rd instar		4th instar		5th instar	
number	Colour	Colour	Days	Colour	Days	Colour	Days	Colour	Days
230/10	grey	green C	10	blackish-grey G	10	grey-green F	4	green F	23
230/31	grey	green C	9	blackish-brown H	8	green C	23	*died in 4th*	
313/11	black	green and black C	4	grey-brown K	16	grey-brown C	5	green C	32
330	grey	not noted	—	green M	12	yellow-brown N	16	green C	4
330/2	grey	grey C	15	green C	22	grey F	20	green C	14
330/13	grey	green C	9	yellowish-green F	13	pale grey F	21	green C	19
330/15	grey	green C	9	grey-black H	14	green C	12	not noted adult green H	48
330/21	grey	green C	9	grey H	14	green C	12	—	—
330/28	grey	green C	8	grey-brown E	13	green C	8	—	—
330/29	grey	green C	8	grey E	13	green C	8	—	—
330/30	grey	grey C	13	green C	21	grey E	20	green C	20
330/33	grey	green C	8	brown P	13	green C	8	—	—
331	grey	not noted M	—	green M	16	green M	23	grey-black N	12
								adult green C	18
332	grey	grey	16	green M	23	brown N	10	green C	8
337	grey	green M	10	green M	23	yellow-brown N	7	green C	7

The figures in the columns under " days " refer to the number of days after which the colour was noted, counting from the date on which the environment was changed. The capital letters in the columns under " colour " refer to the various conditions :—

C.—Celluloid cylinders over growing grass.

E.—Celluloid cylinder on dry sand ; fed by means of blades of grass, one end of which stood in water.

F.—Celluloid cylinder on wet sand ; fed as in E.

G.—Galvanized wire gauze cylinder about 4in. by 4in. ; fed as in E.

H. —Celluloid cylinder on red flower of Canna, no other food.

K.—Glass lamp chimney on wet soil ; fed twice a day only.

M.—Galvanized wire gauze cylinder 4in. by 4in. over growing maize.

N.—Galvanized wire gauze cylinder, 4in. by 4in., on board ; fed twice a day only.

P.—Wire gauze cylinder painted green on green board ; feeding as in E.

THE CAUSES UNDERLYING THE DEVELOPMENT OF THE *GREGARIA* CHARACTERS.

General considerations and theories.

The physiological aspects of the transformation of the phases have not been adequately studied, but they present an interesting field for students equipped for biochemical and exact experimental work. The theories which agree best with the observed phenomena are presented in the following paragraphs in order to stimulate further work. The explanations are partly of a speculative nature, and some of them have already been suggested by Plotnikov and Uvarov.

The essential Characteristics of Life under crowded Conditions.

To those who have not seen these insects alive, the term crowding probably conveys a very inadequate idea of the conditions of existence in cages containing large numbers. Crowding invariably results in enormous activity. Whereas an individual isolated in one half of a cage leads a life of lazy idleness, its fellows in the other compartment, separated by a gauze partition only, live a life of intense activity that could perhaps best be described as a frenzied effort to escape from some relentless, inwardly pursuing force. This activity depends upon the climatic conditions, and is controlled largely by temperature, varying in direct proportion with the temperature up to a certain point. In cool weather there is very little activity. At night the insects usually sit huddled together; at the hottest time of the day they may be seen resting with their heads upwards on plants in the field, but this quiescence in great heat is not often seen in cages.

The activity of hoppers in the field takes the form of migration in bands or swarms, but it includes fighting to get at the food and cannibalism. In the cages there is, at effective temperatures, an endless running up the side of the cage and dropping down again from the ceiling, and in addition, a great deal of continuous jumping, especially against the glass doors when the sun is shining on them. When one hopper starts to feed, several others try to nibble at the leaf in the same spot, although there is plenty of room to feed elsewhere, so that feeding nearly always consists of a lively scramble accompanied by violent kicking, tugging and jumping.

It is a common occurrence at the time of hatching of *L. m. migratorioides* to see eight or ten hoppers, a week or two old, sitting around the opening of an egg package, each eating an emerging hopper that is as yet unable to jump. Many individuals are also eaten while undergoing moults, and the exuviae are usually also devoured. But the cannibalism seems to be subject to at least one code of ethics: that you may only eat your neighbour if you can catch him in a state of helplessness due to moulting or some accident, such as getting caught in the door.

It is evident that this violent activity is due to mutual stimulation, but it is not clear whether this is due to visual perception, actual contact, or possibly to perception by the olfactory sense-organs. One of the characteristic features of a large swarm of hoppers is that it has a very distinct odour which some locust officers claim to be able to detect at a distance. The writer is of the opinion that the causes of gregariousness are to be sought not only in the reactions to physical stimuli, such as body temperature and the visual perception of other insects, important as these may be, but that certain far more obscure elements, which may even be of a psychological nature, also enter into the problem.

The migratory locusts have the power to increase rapidly under favourable conditions, and the strong instinct to gather together and move together in swarms. In the cages the individuals cannot escape from one another; in nature they could readily do so, but we find small lots consisting of *solitaria* and *transiens* hoppers

obstinately moving together instead of scattering in all directions. Two species of non-migratory grasshoppers were also crowded into cages, but they showed no tendency to develop the violent activity characteristic of the migratory species.

This activity leads to a greatly increased rate of metabolism : there must be nervous activity to produce the muscular work ; the muscles need more food, circulation of the blood must be increased, and so on. Meanwhile, the black and orange coloration develops, and this doubtless causes a rise in the body temperature, as compared with that of a green or grey hopper, due to the greater absorption of heat by the pitch black cuticula. Possibly this high rate of metabolism has certain features in common with the condition described as fever in a vertebrate. As the body temperature rises, the moisture requirements increase, leading to the voracious appetite for all manner of moist substances that is characteristic of the hoppers of the phase *gregaria*. The gregariousness leads the organism into a kind of vicious circle from which it cannot escape : activity leading to black coloration, which causes a rise in body temperature, and this in turn producing still greater activity.

The Theory of Locustine Production.

The black coloration which gives the phase *gregaria* its characteristic appearance is largely of a cuticular nature. Some of the orange is also deposited in the cuticula, and the exuviae of *gregaria* hoppers can always be recognized. Grey and green hoppers cast off exuviae that are practically colourless, but exuviae with a good deal of black on them were obtained from hoppers that became black in painted boxes in the case of *L. m. migratorioides*.

The process of moulting is an important physiological process not merely concerned with an increase in size, but also partaking of the nature of an excretory process. As a result of the excessively high rate of metabolism obtaining in swarm life, the muscles and other tissues produce a surfeit of excretory products that cannot be disposed of by the Malpighian tubules, and these -or their derivatives-- are deposited in the cuticula in the form of a definite pattern of black pigment that is always associated with orange or yellow or both.

In order to simplify the discussion, and to give more definite expression to this theory, the term *locustine* is proposed for the products of this excessive metabolism which lead to the development of the *gregaria* coloration.

If the orange and black type of coloration is due to the presence of locustine, and the *solitaria* types can only develop in its absence, it follows that we should find intermediate types of coloration in hoppers which have lived partly in isolation and partly in swarms, and these are described as *transiens*. The amount of orange and black is in direct proportion to the amount of locustine produced by the organism.

The black colour of the first instar hopper of the phase *gregaria* appears an hour or less after hatching, therefore it could not possibly be due to the activity of the hopper itself, nor could we conceive of the embryo jumping about in the egg to produce the locustine. In a former publication (Faure 1923), the writer stated that the first stage hopper apparently inherited the phase colour of its parents, but this should be modified in the light of the locustine theory. It is not a case of inheritance of characters passed on to the progeny in the usual way through the germ cells, but rather a passing on of locustine from the female to the embryo in the nutritive yolk of the egg.

The process of locustine production does not cease at the end of the hopper stages, but continues during the flight activities of the adults. We may therefore visualize the blood and tissues of the *gregaria* female as being more or less saturated with locustine ; therefore the nutritive yolk of the eggs must also receive the locustine. During its development the embryo digests the yolk, and the locustine finds its way into the cuticula to produce the black characteristic of the first instar.

If the black first instar hopper leads a life of activity, it produces its own locustine, and this results in a second instar coloration of black and orange. If it is isolated and leads a life of ease, there is no locustine production, and after the black cuticula derived from the mother is cast off at the first moult, the hopper appears in its second instar with the coloration characteristic of the phase *solitaria*.

The *gregaria* characteristics are not always lost completely at the first moult in individuals living in isolation. Possibly this may be due to variations in the amount of locustine derived from the mother through the yolk, or to individual variations in the ability to produce orange and black out of small quantities of locustine. In the great majority of cases, the *gregaria* coloration disappeared at the first, second or third moult in hoppers that were isolated and left undisturbed.

We have seen that a small percentage of pitch black hoppers was obtained in the F_3 generation of the crowded progeny of *L. m. migratorioides* ph. *solitaria*. This field material was in all probability descended from a race that had not produced the *gregaria* characters for a long series of generations, therefore we may assume that locustine was not present in it in an appreciable amount. The F_1 progeny, crowded, immediately began producing locustine in sufficient quantity to show a large percentage of *gregaria* coloration in the fourth and fifth instars, but the F_1 adults had little exercise, therefore the locustine content declined in them and their eggs probably did not contain enough to show as black cuticula on the F_2 hoppers of the first instar, which were grey like those of F_1. Not until the F_3 generation hatched did black hoppers of the first instar make their appearance, and then only about 10% were black, and in the F_4 and F_5 there was also only a small percentage of black. The only explanation that appears to fit the case is that there must have been a gradual accumulation of locustine through the succeeding generations.

In the case of *L. pardalina*, there was also a distinct increase in the percentage of black hoppers in the succeeding generations of the crowded progeny of phase *solitaria* from the field (Tables I and II, pp. 303, 306).

An interesting exception to the rule that the progeny of *solitaria* adults are largely grey in *L. pardalina* was noted in 1929. In the cage L.p. 254 a "winter swarm" was reared from 14.vii.29 to 9.ix.29; on the latter date there were 97 hoppers in the cage (18in. by 9in. by 15in.) and they were classified as 87% *solitaria*, 11% *transiens* and 2% *gregaria*. About 36 females and 24 males were left in the cage, and their eggs were wetted in November. About 600 hoppers hatched between 23rd November and 5th December, and I was surprised to note that about 90% were black. At first this result seemed to contradict the general rule, since 87% of the parents had been of the *solitaria* type as hoppers, but I am now convinced that it supports the locustine theory.

The hottest weather of the year in Pretoria is usually experienced in October and November, and during this period the adult locusts were kept together under moderately crowded conditions. Notes were not taken on their activity, but they would certainly have been far more active than isolated locusts. The processes leading to the production of locustine were already in operation before 9th September, when the census of the parents was taken, as shown by the 13% *transiens* plus *gregaria* hoppers found on that date, and they continued until the eggs were laid in November, with the result that the eggs contained enough locustine to produce hoppers of which 90% showed the black colour of *gregaria*.

A Classification of the Types of Coloration in Locust Hoppers.

In the phase *gregaria*, the coloration is more or less constant: first instar usually black, other instars black plus orange or yellow, or black plus both orange and

yellow. This type of coloration is due to excessive metabolism, and is therefore called the *hypermetabolic* coloration.

In the phase *solitaria*, certain colours are developed in imitation of colours strongly predominating in the environment, such as dirty white, black, grey, yellow and brown; for this group the name *imitative* coloration could be used.

The green colour of the phase *solitaria* appears to develop only in hoppers supplied with an abundance of succulent green food in a moist atmosphere; for this the name *nutritional* coloration is proposed.

It will readily be understood that these three groups of coloration do not always lend themselves to rigid separation; in fact they often intergrade into one another in one and the same individual. In grey wire gauze cages containing growing food, one found hoppers which were partly green, and partly grey in imitation of the grey gauze. The *transiens* types show a great variety of different combinations: they are hoppers with a poorly developed type of *gregaria* coloration, combined with green or a variety of imitative colours.

Zolotarevsky (1929) regards green as the basic coloration of the phase *solitaria* in *Locusta migratoria*, and believes that chestnut and especially grey in solitary hoppers indicates a tendency to transform into *gregaria*. The writer has found no evidence supporting this interpretation in the field or in breeding cages during his observations on *L. m. migratorioides* and *L. pardalina*; the phase *solitaria* exhibits an endless variety of coloration in the hopper stages, and these depend upon the conditions of the environment.

Zolotarevsky (1929) also believes that subdivisions of the phase *transiens* can be recognized largely on the basis of coloration, green being characteristic of *dissocians* and chestnut or grey typical of *congregans*. The writer's breeding experiments with both *L. pardalina* and *L. m. migratorioides* do not support this view. If *gregaria* hoppers are isolated, they will become green only under conditions where an abundance of succulent food is available in a moist atmosphere; in other environments they will not become green. Conversely, when green hoppers of *L. pardalina* from the field were crowded together (see p. 308, Table III, Nos. 741 and 742) they lost their green, and acquired greyish-black, poor orange and black (*transiens*), and good orange and black (*gregaria*), giving the same results as grey *solitaria* hoppers. Evidently the green and the grey types are both equally susceptible to the effects of crowding and there is no reason to suppose that the one has a greater tendency to transform into *gregaria* than the other.

As for the structural characters used by Zolotarevsky in separating *congregans* from *dissocians*, these appear to the writer to be too variable and intangible to be of practical value. In his schematic representation (1929, fig. 6) Zolotarevsky himself admits this, since he summarizes the differences as "bossue" and "peu bossue" in referring to the pronotum.

The Morphological Differences in Adults.

Although differences in colour also occur, the striking characters differentiating the adults of the two phases are found in the shape of the pronotum and the length of the wings. There is such an intimate connection between *gregaria* coloration in the nymphs and *gregaria* characters in the adults that the processes causing the former must of necessity also be concerned in the production of the latter. But while the same violent activity must be regarded as the primary cause of these modifications, it is doubtful whether locustine is a factor in this case, and detailed anatomical studies might reveal mechanical principles as the factors directly responsible.

The obvious differences between an extreme *solitaria* adult and one of the extreme *gregaria* type are that the latter has relatively longer wings and a pronotum that

appears to have been tightly constricted during development, and thereby prevented from acquiring the higher arched keel of the former. This is very striking in *L. m. migratorioides*. It seems reasonable to assume that the enormous amount of muscle contraction involved in the constant activity of the legs of the hopper tends to alter the shape of the thorax in such a way as to bring about the constriction of the pronotum. Similarly the increase in the length of the wings may be connected with the great muscular activity going on in the thorax during their development.

The flight activities of adults have been mentioned above as contributing to the production of locustine. If the contraction of the muscles of flight tends to produce a pinched pronotum, this effect can obviously only be carried through the egg and the hopper stages to the next generation of adults, because the form of the pronotum is fixed in the adult as soon as it has hardened after the final moult. There was a distinct tendency towards a progressive increase in the development of adult *gregaria* characters in the series of cage-bred generations of *L. m. migratorioides* as shown above (Tables X and XI, p. 346). That the same occurs in the field is shown by the differences found in the biometrical data of the Makoni material and the extreme *gregaria* material from East Africa.

Zolotarevsky (1929), working in Madagascar, found that *Locusta migratoria capito*, Sauss., has its important permanent areas of incipient swarming in the south of the island, and concluded that the north and east are only invaded by the progeny of swarms originating in the south or south-west. In comparing the biometrical data resulting from measurements of adults from various localities, he arrived at this interesting conclusion : that the development of the extreme *gregaria* characters varies in direct proportion with the distance from the area of origin of swarms in the south. In other words, as the infestation spreads further north in succeeding generations there is a progressive increase in the acquisition of extreme *gregaria* characters.

This raises the question of whether we are dealing here with the inheritance of acquired characters. The answer would be in the affirmative if it could be proved that the *gregaria* characters, once properly developed, tended to become fixed in the succeeding generations. On the contrary, these characters will persist only as long as the insects are living in dense crowds, *i.e.*, only if maintained by excessive activity, and they disappear as soon as the locusts lead an isolated existence.

These species have inherent in their make-up the ability to develop the *gregaria* characters. Variation in this direction is induced by the intense rate of metabolism characteristic of life in dense crowds, and this variation becomes progressively greater through succeeding generations until the extreme is reached. At any moment the removal of the cause—swarm activity—will result in the reappearance of the *solitaria* characters.

In a sense the *gregaria* characteristics might be described as the external evidence of semi-pathological conditions resulting from excessive metabolism : the orange and black are due to metabolic products deposited in the cuticula and the pinched pronotum and long wings are modifications brought about primarily by excessive muscular exercise.

Experiments and Observations.

If the excessive rate of metabolism resulting from muscular activity is the cause of the variation towards *gregaria*, one individual reared by itself should develop these characters provided that it can be forced to be as active as its fellows reared in a dense crowd. Conversely, the individuals reared in isolation must lose the *gregaria* characters if they are inactive. The latter experiment is simplicity itself, and many examples have already been given which show that the vast majority of those isolated lose the *gregaria* characters. But the problem of forcing an isolated individual into activity has proved exceedingly difficult.

Hoppers in a Crowd of another Species.

Given crowds of hoppers of several species of migratory locusts, it is an easy matter to place a few individuals in a crowd of another species. If they are fortunate enough to survive in the scramble, these hoppers are easily recognized, because those of the four species occurring in South Africa may be readily distinguished from one another even in the phase *solitaria*, while they are conspicuously different in the phase *gregaria* (see Pls. xiv–xix, figs. 6, 32, 40 and 55).

Several attempts were made to rear a few individuals of *L. pardalina* in crowds of *L. m. migratorioides*. In two cases some of the hoppers survived long enough to give results :—

(1) Seven *L.p.* of first instar, grey, placed in cage 18in. by 9in. by 15in. containing about 400 hoppers of *L.m.m.* ; four survived to the fifth instar, all good *gregaria* types.

(2) Six *L.p.* of first instar, grey, in 18in. by 9in. by 15in. cage with about 400 *L.m.m.* ; one survived to fourth instar and was described as good *gregaria* type.

In both cases the surviving hoppers acquired the *gregaria* coloration, but they were certainly not reared in isolation. They were forced into activity by those of the other species, so that an intense metabolism was in all probability the factor which produced the *gregaria* characters. The crowded existence required need not be intra-specific, since inter-specific crowding produces the same result. But if other elements included in the condition called crowding enter into the problem, such as crowd temperature, crowd moisture, or cannibalism, these were by no means excluded ; therefore we cannot claim to have proved that muscular activity is the important factor.

In the following tests carried out with *L. m. migratorioides* the same result was obtained, all the surviving hoppers showing a strong development of *gregaria* characters :—

(1) Five *L.m.m.* first instar grey in cage 18in. by 9in. by 15in. containing about 250 hoppers of *Schistocerca gregaria*, of which about 80 survived ; two of *L.m.m.* reached the fifth instar and were described as good *transiens*, near *gregaria* type.

(2) Three *L.m.m.* first instar grey in cage 6in. by 4½in. by 6in. with about 65 *L.p.* ; one survived to fourth, *gregaria* type.

(3) Three *L.m.m.* first instar grey in cage 6in. by 4½in. by 6in. with 50 *L.p.* ; one survived to fourth, *gregaria* type.

Hoppers isolated in Cages surrounded by Crowds.

The close proximity of crowds of hoppers had no apparent effect on isolated hoppers in cases where the two cages were separated by a vertical partition of wire gauze. The standard cages used (Pl. xxxvi, figs. 189–191) were divided into two halves in this way. In many cases we had a crowd in one half and a single individual in the other, but the isolated hoppers showed no tendency to become active and they invariably remained or became *solitaria*.

A small series of tests was undertaken with isolation cages placed on the floor of a cage containing a crowd of hoppers in such a way that the crowd would be crawling over the smaller cages more or less constantly during the periods of activity. In these, five hoppers of *L. pardalina* survived to the fifth instar :—

A. Small tent-shaped cage of wire gauze, 4in. by 3in. by 2½in., fixed on floor of cage 18in. by 9in. by 15in. containing about 300 hoppers of *L.p.* Two hoppers, first instar black, were reared to the fifth ; one described as fair, the other as good *gregaria* type.

B. Small rectangular cage of wire gauze, 3in. by 3in. by $2\frac{1}{2}$in., on floor of large cage 3ft. by $2\frac{1}{2}$ft. by $2\frac{1}{2}$ft. containing about 2,000 *L.p.* One hopper put in as first instar black survived to the fifth and was described as good *gregaria*.

C. Cages of glass, 8in. by 4in. by $1\frac{3}{4}$in., on floor of large cage 3ft. by $2\frac{1}{2}$ft. by $2\frac{1}{2}$ft., containing about 500 adults and hoppers of *L.m.m.* Two hoppers put in as first instar black survived to fifth; one fair *transiens*, the other light grey *solitaria*.

It was not practicable to take detailed notes on the activity of the hoppers in these experiments. The results indicate that those in the gauze cages were apparently subjected to the factors which produce the *gregaria* coloration, because all three surviving to the fifth instar retained the *gregaria* characters. To a certain extent direct contact entered into the case here; the small cages were made almost entirely of gauze, and the isolated hopper, sitting on the gauze with its claws and parts of the tarsi projecting through it, would certainly be touched by the feet of the crowd passing over it. In these experiments some of the other component parts of the crowd environment, such as the odour, were also not eliminated.

In the glass cages direct contact was eliminated, and this seems the most acceptable explanation of the difference in the results, but it must be admitted that the gauze and glass cages were not placed in cages containing crowds of equal density, and that these experiments were carried out on a very small scale.

Attempts to force isolated Hoppers into Activity.

In view of the remarkable activity of the crowded insects, it would appear very easy to place a single individual in a cage by itself and to force it into activity by means of some simple mechanical disturbance. Unfortunately this is not the case. If a *gregaria* hopper is taken from a crowd and placed in the jarring apparatus described below, it is exceedingly susceptible to disturbances and jumps violently for a day or two, but this soon wears off and then it becomes a matter of difficulty to get it to jump at all. In order to provide conditions approaching those of swarm life, it is necessary to maintain daily activity over a period of weeks; the ideal would be to keep the hopper active throughout its development from the first to the fifth instar, and this extends over six to eight weeks under outdoor conditions in the summer.

Detailed studies of the reactions to various stimuli under controlled conditions were not carried out, but a number of different methods of stimulation were tried and the results may be of interest to other workers.

Various methods of mechanical disturbance all showed that the hoppers very soon get accustomed to something that makes them jump well at first. A cage of glass was constructed with a metal floor that could be moved up for about half an inch from below; the glass (or celluloid) sides are necessary to force the hopper down on to the floor again after the jump. Violent tapping of this metal floor sent the hopper off beautifully at first, but it soon became indifferent to the shocks and would attempt to feed in spite of them, carrying a piece of food in its jaws when thrown up off the floor, but not making any effort to jump at all.

Tickling with bristles from a brush, or with feathers, was tried in the hope that it might be practicable to construct a cage with a revolving brush from which the hopper could not escape, but this method gave no promise of success because the insects took very little notice of the disturbance after it had been repeated for some time.

If placed on a metal plate over an electric lamp, the hoppers jump violently when the temperature reaches a point at which the plate can barely be touched by the human hand, and this method seemed promising at first. The cages were made

of glass sides, standing on floors of galvanized iron. Experience soon showed that the violent jumping was a signal of great distress and hoppers that appeared to be reacting well would usually die after a few days exposure. As the temperature rises they turn their bodies sideways against the metal to get as much warmth as possible. Then they rise up on their tarsi, and finally stand on the claws only, lifting first one leg and then another that gets too hot. But the reaction of jumping does not begin until the plate is so hot that prolonged contact would result in serious harm. It would therefore appear to be impossible to obtain a proper jumping reaction by this method, even if one had a delicate apparatus to turn off the heat as soon as jumping commences, because the hopper only seems to jump when it is in danger of burning to death.

A variation of this method was tried for some weeks, but it also proved a failure. Hoppers were confined in cylinders of celluloid about 12in. high and 6in. in diameter tacked to a circular piece of wood. If exposed to the sun they would commence jumping as soon as the surface of the wood became too hot to be comfortable, and they could be left to jump for five to ten minutes without danger of injury. The total amount of activity obtained during the periods of exposure did not approach that going on in crowded cages, and only a few hours of exposure could be worked in during an average day owing to partial cloudiness, cool breezes, and other factors which reduced the activity of these isolated hoppers to an infinitely greater extent than that of the hoppers living in crowds. A number of hoppers of *L. pardalina* were successfully reared to the adult stage in these cages without developing or retaining the *gregaria* characters, but the sum total of their muscular activity probably did not amount to more than 5% of that of their fellows reared in crowds.

Allowing fine dry sand to run slowly through a funnel into a celluloid cylinder containing a hopper gave reactions that appeared at first to be promising. The sand was allowed to run in until it filled about half the cylinder, and after an interval of about 10 minutes it was cleared out and allowed to run in again. For the first few days the hoppers subjected to this bombardment were very active, but they did not thrive, probably because they were injured by the falling sand and sometimes became buried under it.

Various circular glass flasks were tried under conditions that kept them moving slightly, and the hoppers walked about a good deal trying to get up the smooth sides, but they did not react by jumping to any extent. *Gregaria* hoppers of the first instar (*L. pardalina*) were confined in cylindrical cages about 2in. in diameter and 8in. high, lined entirely with mirrors. For a couple of days there was a fair amount of jumping reaction, indicating that visual perception of its own movements had the effect of causing the hopper to jump, but this reaction very soon ceased and the hoppers did not thrive in these cages, which were kept outdoors under a canopy of calico.

Electric shocks were also tried on a small scale without any promise of success. When placed in a field of induced electricity on moist sand, the hoppers showed no tendency to jump even when the intensity was such as to cause a sharp jerk to the human hand. If a current of electricity was passed through them the insects reacted violently, but the first result seemed to be to break off both hind legs. The chitinous exoskeleton appears to provide excellent insulation.

Small Cages of Celluloid.

While making celluloid cylinders for the experiments on the green colour, Mr. E. E. Schaefer constructed a small hat-shaped cage of celluloid, about 3in. in height and similar in shape to those figured (Pl. xxxviii, fig. 201). He attached this cage to one of the 18in. by 9in. by 15in. cages in such a way that the base of the cage rested against the glass door, in order to watch for possible activity developing in the black *L.*

pardalina hopper of the first instar confined in it. The hopper lost its *gregaria* characters in the second or third instar, and after that the observers took no particular interest in it, although it was regularly fed. Then to our surprise the hopper developed quite a good *transiens* type of coloration in the fifth instar. The cage had a sloping floor, and we noticed that the hopper often performed a sort of mad dance on this, trying to move up and continually slipping back again.

This led to the making of numerous other small cages of celluloid with floors sloping at different angles, and these were placed against the glass doors of cages containing crowds, but no further cases of retention or development of the *gregaria* coloration were observed. The presence of large numbers of actively jumping locusts on the other side of a sheet of glass did not appear to have any stimulating effect upon the hoppers isolated in these small celluloid cages; we concluded that what little activity did develop was largely due to the fact that they tried to walk on the smooth floor and sides and kept slipping back. The development of *gregaria* characters in the original hopper was regarded as an exceptional occurrence, because we were unable to duplicate it.

Celluloid has many advantages: the surface is too smooth for the larger hoppers to walk on at an angle; unlike glass, it does not get too hot to leave outdoors in the sun; it can be made up into many shapes and sizes with the aid of acetone. The disadvantage is that it perishes after a few months' exposure to the elements.

The Jarring Apparatus.

Having these promising celluloid cages, the next step was to try to obtain activity by jarring at frequent intervals throughout the day. For this purpose a piece of apparatus was constructed on the "home made" principle (figs. 199 and 201). The essential features were cages of celluloid, and a rotating piece of strap-iron which jarred the cages violently about 20 times a minute.

The cages measured about $4\frac{1}{2}$in. by $2\frac{1}{2}$in. at the end attached to their common base, and about 4in. by $1\frac{3}{4}$in. at the smaller end, and were about 4in. in height. The floor sloped at a moderate angle; in the floor and in the roof there was a row of small air holes. At the upper side of the front end a hole about $\frac{1}{2}$in. in diameter served as a door, and it was closed by means of a piece of perforated zinc.

This apparatus was kept outdoors in the sun, but on hot days an awning of calico was stretched over it. The hoppers were fed three or four times a day on green grass cut into pieces about $\frac{1}{8}$in. in diameter; if larger pieces were used the insects would sit on the food and allow themselves to be thrown about in the cage. Water was occasionally sprinkled over the cages, but if water accumulated in the cages the hoppers seemed to cling to the celluloid instead of jumping and walking.

The motor was started in the mornings at about 8.30 a.m. and kept running until about 5 p.m. with an interval of about one hour at noon. On rainy and cool days there was practically no activity, therefore the machine was usually stopped in such weather. Moulting caused a good deal of trouble while we tried to remove the individuals which were about to moult, in order to allow them to moult undisturbed. Later the assistant in charge came to the conclusion that the insects would delay the moult until the lunch interval. This seemed difficult to accept, and it may have been coincidence, but the plan of removing those about to moult proved difficult to carry out in practice, therefore the assistant's method was followed. Casualties due to disturbance of the moult were exceptional.

Compared with the hoppers reared in isolation in gauze cylinders, those kept in the jarring apparatus had a considerable amount of muscular exercise, but their activity was very poor compared with that of the insects reared in a crowd. At times of the day when their neighbours crowded in adjoining cages were jumping and walking actively, those in the jarring apparatus would merely give an occasional

listless jump and move their legs to and fro in an effort to get a foothold on the smooth celluloid. If one that had lived for some weeks in a crowd were transferred to the agitator, it would jump very violently for a day or two; then it would die, or grow accustomed to the jarring and show the same poor reaction as the rest.

If the experiment were repeated, one should try much larger cages, possibly large enough to permit a jump of about 18 inches, because some of the hoppers probably injured themselves by jumping violently against the top of the cage.

There was a very heavy mortality in these cages, only about 7% of the hoppers surviving to the fifth instar. This was partly due to the heat and probably in large measure to lack of moisture, because the food wilted very quickly. If the whole apparatus could be kept in a chamber under controlled conditions of humidity and temperature, a larger percentage of hoppers would probably survive. It seems essential to have the apparatus in direct sunlight—or at least in artificial sunlight—because hoppers kept under a thatched roof do not thrive, and great difficulty was experienced in rearing them in incubators.

Results obtained in the Jarring Apparatus.

The jarring apparatus was in operation from December 1930 to April 1931; during this period there were several stoppages of about a day for repairs, and on rainy days the motor was also stopped. Details of weather conditions are not included here because many controls on these experiments, namely hoppers in undisturbed isolation and in crowded cages were reared at the same time in adjoining cages, and these gave the usual results.

Altogether 342 hoppers of *L. pardalina* were placed in these cages, but only 26 survived to the fifth instar, and the great majority lived for only four or five days. Hoppers of both phases were placed in the apparatus, as follows:—

	1st instar		2nd instar	
	placed in apparatus	survived to 5th	placed in apparatus	survived to 5th
solitaria ...	64	—	10	—
transiens ...	48	—	—	—
gregaria ...	108	14	112	12
Totals ...	220	14	122	12

It is interesting that all survivors were of the *gregaria* type when placed in the apparatus, suggesting the possibility of greater resistance to disturbances in this phase.

Table XVII contains the details concerning the 26 hoppers which survived to the fifth instar. Some became adults but the results were judged only on the basis of the coloration of the hoppers. Of those that were placed in as first instar hoppers, 6 were described as *transiens* types, or 42·9%, and 8 were of the *solitaria* type, or 57·1%. Twelve that were put in as second instar hoppers survived to the fifth; of these 2 were *gregaria*, or 16·6%, 5 were *transiens*, or 41·7%, and 5 were *solitaria*, or 41·7%.

TABLE XVII.

L. pardalina in jarring apparatus.

L.p. number	Date placed in apparatus	2nd instar	3rd instar	4th instar	5th instar	Number of days in apparatus
		Hoppers put in as first instar *gregaria* type				
565/35 ...	4.ii.31	*solitaria*	grey *solitaria*	grey *solitaria*	grey *solitaria*	40
565/39 ...	3.ii.31	grey *solitaria*	grey *solitaria*	*solitaria*	poor *transiens*	30
565/41 ...	3.ii.31	grey *solitaria*	grey *solitaria*	grey *solitaria*	grey *solitaria*	34
724/24 ...	9.ii.31	*solitaria*	—	poor *transiens*	poor *transiens*	39
724/25 ...	5.ii.31	grey *solitaria*	grey *solitaria*	grey *solitaria*	grey *solitaria*	43
743/15 ...	9.iii.31	*transiens*	*solitaria*	—	good *transiens*	65
743/16 ...	14.iii.31	*transiens*	—	—	poor *transiens*	60
743/18 ...	4.ii.31	*solitaria*	*transiens*	*transiens*	*transiens*	38
743/19 ...	4.ii.31	*solitaria*	*solitaria*	*solitaria*	*solitaria*	55
745/2 ...	29.i.31	*solitaria*	*solitaria*	grey *solitaria*	grey *solitaria*	49
745/4 ...	7.i.31	*transiens*	grey *solitaria*	grey *solitaria*	grey *solitaria*	30
745/6 ...	29.i.31	*solitaria*	*solitaria*	*solitaria*	*solitaria*	51
745/7 ...	10.iii.31	*solitaria*	*solitaria*	*solitaria*	*solitaria*	64
745/12 ...	3.ii.31	grey *solitaria*	poor *transiens*	poor *transiens*	poor *transiens*	50
		Hoppers put in as second instar *gregaria* type				
565/37 ...	16.ii.31	—	*gregaria*	*gregaria*	good *transiens*	28
565/40 ...	11.ii.31	—	*solitaria*	*solitaria*	*solitaria*	50
724/2 ...	12.xii.30	—	*transiens*	*transiens*	poor *transiens*	42
724/9 ...	9.xii.30	—	*solitaria*	*solitaria*	*solitaria*	36
743/9 ...	11.ii.31	—	*gregaria*	*gregaria*	*gregaria*	34
743/12 ...	14.ii.31	—	good *transiens*	good *transiens*	*gregaria*	33
743/17 ...	13.ii.31	—	*transiens*	*transiens*	*solitaria*	37
743/20 ...	12.ii.31	—	poor *transiens*	poor *transiens*	fair *transiens*	35
745/3 ...	17.i.3	—	*solitaria*	*solitaria*	*solitaria*	61
745/5 ...	14.ii.31	—	poor *transiens*	*solitaria*	*solitaria*	35
745/8 ...	9.i.31	—	poor *transiens*	*solitaria*	poor *transiens*	59
745/9 ...	10.ii.31	—	poor *transiens*	good *transiens*	good *transiens*	33

Comparing these results and those obtained with hoppers reared in isolation in wire gauze cylinders, painted boxes and celluloid cylinders (excluding those reared

for tests of the hypothesis concerning Mendelian inheritance), we find the following data :—

	Number surviving to 5th instar				Percentages		
	sol.	*trans.*	*greg.*	Total.	*sol.*	*trans.*	*greg.*
1st instar *gregaria* in jarring apparatus	8	6	—	14	57·1	42·9	—
1st instar *gregaria* in undisturbed isolation	135	2	2	139	97·1	1·45	1·45
2nd instar *gregaria* in jarring apparatus	5	5	2	12	41·7	41·7	16·6
2nd instar *gregaria* in undisturbed isolation	19	2	—	21	90·5	9·5	—

A very interesting feature in Table XVII is that the *gregaria* coloration was first lost and then regained by six of the hoppers. This lends support to the locustine theory. In the first instar the hoppers are to a certain extent able to crawl up the sides of the cages ; therefore they do not slip back so readily as older hoppers. In all probability the muscular exercise obtained in this apparatus consisted largely in crawling about in an effort to get a foothold rather than in actual jumping. During the first instar little locustine would therefore be produced, and in the second the *facies* would be that of *solitaria*. With the increase in weight the hopper would get relatively more exercise, due to slipping in the later instars, and this probably increased locustine production and caused the return of *gregaria* characters.

In conclusion, the number of hoppers reared to the fifth instar is rather small for definite conclusions. However, there seems to be no reason to doubt that the much greater percentage of *transiens* types obtained in these cages, as compared with ordinary isolations, was due entirely to the mechanical disturbance and the resulting muscular exercise. Considered in the light of the other data presented in this paper, the results in Table XVII may be regarded as a strong indication of the substantial correctness of the locustine theory.

The Effect of Temperature.

It is well known that the temperature of their environment has a profound effect upon the behaviour of locusts, determining to a large extent the commencement, intensity and cessation of their activities ; the literature on these aspects of the effects of temperature is discussed by Uvarov (1928). In an attempt to analyse the factors which may be responsible for the development of *gregaria* characters under crowded conditions, temperature obviously calls for careful study. There is no doubt that the *gregaria* characters are more readily developed in hot weather than in cool weather, as is proved by the results obtained from summer and winter crowds. This is due to the fact that activity varies in direct proportion with the temperature, within certain limits.

The question arises whether the *gregaria* characters could not be produced by rearing a locust in isolation at a suitable temperature. If temperature promotes activity, the isolated hopper should also become active. Again, the *gregaria* characters might be due to the increased temperature, obtaining in the swarm when it is densely clustered for the night, and to the increased body temperature of its members resulting from their activity.

In the field, isolated hoppers of *L. pardalina* must be subjected to very high temperatures, especially in periods of drought, when there is often very little green

vegetation in their permanent habitat. At such times the insects are very scarce, but the specimens taken are of the extreme *solitaria* type. Large swarms, incipient swarms and completely isolated individuals are at times to be found a few miles, or even a few thousand yards apart on veld that is approximately in the same condition, indicating that factors such as temperature, moisture and food supply do not enter into the problem of the *gregaria* characters as direct causal agents.

In the breeding experiments, the isolation cages were kept side by side with those containing crowds; therefore the insects reared in them must have been subjected to the same air temperature and solar radiation, except in so far as those in the crowds modified their own microclimate. The isolated individuals remained inactive at all temperatures and they did not acquire the *gregaria* characters.

TABLE XVIII.

Locustana pardalina: Hoppers kept in incubators at constant temperatures.

L.p. number	Temperature and treatment	Number of hoppers at start, instar and colour	Number of hoppers surviving and instars. Figures in brackets: number of days after start	Description of surviving hoppers		
				sol.	*trans.*	*greg.*
331	30–32°C.;	1 grey first	1 fourth (28)	1	—	—
332	constant	40 grey and black first and second	2 fourth ... ... 3 third 2 second (15)	1	3	3
393	30–32°C.;	1 black first	1 fifth (49)	1	—	—
392	constant	75 black first	8 second (12)	—	—	8
441	35°C. day	1 black first	1 fourth (25)	1	—	—
440	25°C. night; changed over	25 black first and 2 second *gregaria*	14 third and fourth (19) ...	—	—	14
492	31°C.;	1 black first	1 fourth (21)	1	—	—
496	constant	41 black first	10 third (14)	6	4	—
497	31°C.; constant but left out 1–2 hours daily	1 second *gregaria*	1 fourth (16)	1	—	—
498		50 second *gregaria*	7 fourth and fifth (21) ...	2	3	2
560	27°C.;	1 second *gregaria*	1 fourth (18)	1	—	—
559	constant	38 first *transiens* 8 second *gregaria*	15 fourth (18)	13	2	—
562	31°C.;	1 black first	1 fifth (13)	1	—	—
561	constant	43 black and 2 grey, first	22 fifth (22)	8	7	7

Experiments in Rearing at Constant Temperatures.

Attempts were made to rear isolated and crowded hoppers side by side in incubators at various constant temperatures, but great difficulty was experienced in keeping the hoppers alive. This was probably due in part to the fact that the humidity was not accurately controlled, and to the absence of sunlight, which seems to be essential, especially to *L. pardalina*. The activity developed by the crowds in the incubators could not be noted through the wooden doors, but in opening the chambers one could often see that the insects were exceedingly active. It is probable that an excessive amount of swarm activity developed in the crowds kept at the higher temperatures, and that this contributed largely to the high mortality.

The cages used in these experiments were made of wood and galvanized wire

gauze (fig. 197). One half of a cage was used as a unit ; the dimensions of the half cage were 6in. by 4½in. by 6in. The experiments listed in Tables XVIII and XIX are arranged in groups of two ; the crowd was kept in one half of a cage and one hopper in the other half, with a partition of glass or metal between them. In this way the crowd and the isolated hopper would necessarily be subjected to the same conditions of temperature, light and humidity.

The incubators used were electrically heated chambers, with capsule temperature control. One was provided with ventilation holes, and two were without ventilation. The results were equally disappointing in both the ventilated and unventilated chambers. All the chambers were dark, being closed by means of a glass inside door, and a tightly fitting wooden door outside.

In addition to the 7 pairs listed in Table XVIII, 13 other pairs of cages containing crowds and isolated hoppers of *L. pardalina* were kept in incubators, at temperatures varying from 20° C. to 35° C. In all 13 pairs of cages the hoppers died so soon that no results were obtained. Open tins or jars of water were usually kept in the incubators, and water was occasionally sprinkled in the cages. The hoppers were supplied two or three times a day with an adequate amount of green grass, barley or maize.

In view of the small numbers which survived, the experiments listed in Table XVIII do not warrant definite conclusions. They indicate that hoppers reared in isolation at relatively high constant temperatures will not acquire the *gregaria* characters. Those reared in crowds at these temperatures tended on the whole to retain the *gregaria* characters.

Concurrently with these attempts to rear *L. pardalina* in incubators, a series of tests were also undertaken with hoppers of *L. m. migratorioides* with equally disappointing results. Table XIX contains the records of the six pairs of cages in which a few of the hoppers survived for several weeks.

TABLE XIX.

Hoppers of *Locusta migratoria migratorioides* kept in incubators at constant temperatures.

L.d. number	Temperature and treatment	Number of hoppers at start, instar and colour	Number of hoppers surviving and instars. Figures in brackets : number of days after start	Description of surviving hoppers		
				sol.	*trans.*	*greg.*
244	31°C. ; out for 3–4 hours daily	1 first grey	1 fifth (34)	1	—	—
243		42 first grey	9 fourth (20)	6	1	2
246	30°C. ; constant	1 first grey	1 fifth (25)	1	—	—
245		41 first grey	13 fourth and fifth (25) ...	5	4	4
245A	31°C. ; out for 3–4 hours daily	1 first grey	1 fifth (29)	1	—	—
246A		32 first grey	2 fifth, 2 fourth, 1 third (34)	1	2	2

Although only a small percentage of hoppers survived to the 4th and 5th instars in the cages containing crowds, the results obtained confirmed those recorded above for *L. pardalina*.

Summer and Winter Crowds.

The long diapause in eggs of *L. pardalina* that are kept dry makes it possible to obtain hoppers of this species at all times of the year, and they can be reared under outdoor conditions at all seasons in Pretoria. During the winter, development is considerably slower, but the cold weather experienced in Pretoria does not cause an

appreciably greater reduction in numbers in crowded cages than that occurring during the summer. Activity is greatly reduced in winter, and this is clearly seen in the comparison of crowds of approximately the same density reared in summer and winter.

Table XX contains the records of twelve crowds, arranged in pairs according to the number of hoppers surviving at the census, and the time of the year during which they were reared.* The data show that a much higher percentage of *gregaria* types was invariably obtained in the summer crowds than in the winter crowds of each pair. This applies equally to the pairs in which more than 200 hoppers survived and to those in which only about 50 survived. It was noted that the winter crowds were much less active than the summer crowds. We may conclude that temperature had a profound influence on the activity of the insects: higher and lower mean temperatures caused a respectively greater or smaller variation towards the phase *gregaria* in cages containing crowds of approximately the same density.

Moisture as a Factor affecting Variation towards the Phase *gregaria*.

Parker (1930) reported that food of a low moisture content had a tendency to produce larger and relatively longer-winged individuals than highly succulent food in the case of *Melanoplus mexicanus mexicanus* (Sauss.), and suggested that *Melanoplus spretus* (Walsh) may possibly have been a dry-weather phase of *M. mexicanus*.

Zolotarevsky (1929) stated that *Locusta migratoria capito*, Sauss., was popularly supposed to become abundant in Madagascar as a result of drought. He explained this not as a direct result of feeding on food of low moisture content, but rather as a case of concentration of the phase *solitaria* on islands of green food left around moist depressions at the beginning of the dry season, and thought that the resulting concentration of eggs and hoppers brought about the commencement of transformation into *gregaria*.

Plotnikov (1924) considered the possibility that moisture might be a factor in the production of *gregaria* characters, but concluded that it had been eliminated as such because *gregaria* and *solitaria* occurred in his experiments in moist jars as well as in drier cages.

It is quite possible that the microclimate of a hopper forming part of a dense swarm may have an appreciably higher relative humidity than that of a hopper living in isolation, especially at the times when the members of the swarm are closely crowded. This crowd-moisture may be a supplementary factor favouring the physiological conditions required for the development of *gregaria* characters. It is evident from the experiments of the writer that a very moist atmosphere and an abundance of food of high moisture content are not primary factors influencing the production of *gregaria* or *solitaria* coloration, except in so far as they produce a high percentage of green hoppers, as shown above.

In the writer's experiments, *gregaria* hoppers of *L. pardalina* and *L. m. migratorioides* placed in celluloid on growing grass lost the *gregaria* coloration just as readily as those placed in gauze cylinders on food supplied twice a day only. In celluloid cylinders over growing grass, under a box excluding all light, the *gregaria* coloration developed in the case of one small crowd of hoppers. In cages containing crowds,

* The temperatures were obtained from a meteorological thermograph, kept in a standard screen about 50 yards from the cages. The average maximum and minimum were arrived at by adding together the daily maxima and minima and dividing by the number of days. The mean was obtained by adding together the average maximum and minimum and dividing by two. The records were not quite complete, therefore the data for the missing days were interpolated from the official meteorological records for Pretoria, which were taken about two miles from the University grounds. After making comparisons, it was found that very close approximations could be made by deducting 1°F. from the city records for both maxima and minima.

TABLE XX.

Locustana pardalina: Relation between temperature and activity as expressed by the percentage of *gregaria* hoppers appearing in summer and winter crowds of approximately the same density.

All the crowds listed below were kept in cages of the same size: 18″ × 9″ × 15″.

L.p. number	1st instar hoppers			Period in cage		Census: based on coloration (mainly in 4th and 5th instar)				Temperature for period (in degrees Fahrenheit)				
	Total put in cage	Estimated colour		Date put in	Date censused	Total	Percentage			Number of days	Days for which records interpolated	Average maximum	Average minimum	Mean
		%grey	%black				*solitaria*	*transiens*	*gregaria*					
724	433	90	10	28.xi.30	5.1.31	220	0	2·3	97·7	39	0	86·3	61·2	73·75
529	500	?50	?50	14.iv.30	16.vi.30	266	16	25	59	64	8	70·6	40·6	55·6
325	380	10	90	26.xi.29	15.i.30	151	2	2	96	51	0	82·9	59·8	71·4
574	280	5	95	22.v.30	14.vii.30	186	39·8	26·9	33·3	54	8	67·6	36·2	51·9
253	250	?50	?50	15.xi.29	2.i.30	149	0	5	95	49	0	81·5	59·2	70·4
565	275	85	15	20.v.30	22.vii.30	133	80	16	4	64	16	68·2	36·5	52·4
369	860	5	95	17.xii.29	28.i.30	83	8	17	75	43	0	83·3	59·9	71·6
531	160	?50	?50	14.iv.30	4.vi.30	83	84	8	8	52	8	71·5	41·3	56·4
756	260	?5	?95	2.ii.31	14.iii.31	81	3·7	23·5	72·8	41	4	81·1	59·1	70·1
245	250	?40	?60	14.vii.29	9.ix.29	97	87	11	2	58	0	73·1	42·0	57·5
774	113	5	95	18.iii.31	24.iv.31	51	0	14	86	38	0	77·2	53·8	65·5
593	60	90	10	26.vii.30	10.ix.30	43	100	0	0	47	8	71·6	40·6	56·1

it was the general rule to supply an abundance of cut green food at frequent intervals as required. In hot weather this would also wilt, but it was often thrown in in heaps of fair size, so that it did not wilt so soon as in the cages of gauze used for isolation. The crowds, therefore, had a much more regular supply of succulent food than the hoppers in isolation, and the *gregaria* coloration invariably developed in the crowds.

In the field, both *gregaria* and *solitaria* hoppers of *L. pardalina* are found in places where there is an abundance of succulent food, and under conditions where food seems so scarce that one is puzzled to understand what they live on. There does not seem to be any evidence in this species of a direct relation between food of high or low moisture content and the development of the phase *gregaria*. It is true that widespread invasions of *L. pardalina* seem to occur shortly after good general rains have brought to an end a series of dry seasons, but this probably means that climatic conditions and an abundance of food favour the rapid increase of the species, which leads to incipient swarming as soon as density and numbers permit. But before incipient swarms can be formed, there must be, on the abundance of succulent food, a large population of scattered *L. pardalina* in the phase *solitaria*. Evidently, then, the development of neither *gregaria* nor *solitaria* characters is a result of dry or succulent food.

The Influence of Light.

It is well known that locusts display a strong positive phototropism ; this is equally true of the phases *gregaria* and *solitaria*. It does not seem probable that light could be of importance as a direct factor influencing the development of *gregaria* characters, except in so far as the general growth and activity of the insects may be promoted by sunlight. In the writer's experience, locusts did not thrive when kept in the shade, but this may be due to temperature rather than light.

In the incubator experiments reported above, the *gregaria* characters developed in hoppers reared in darkness. Under a box admitting no light a small crowd of *L. pardalina* hoppers kept on growing grass also produced a few individuals of the *gregaria* type. These observations indicate that light is not necessary for the production of the orange and black coloration.

Another observation not bearing on the question of phases is of interest in this connection. La Baume, as quoted by Uvarov (1928), believed that light was one of the factors which influence the intermediate moult that takes place at the moment when the hopper emerges from the egg package. I have found that hoppers of *L. pardalina*, *L. m. migratorioides*, *Nomadacris septemfasciata* and *Schistocerca gregaria*, complete this moult without difficulty in the darkness of the chambers in which the eggs were often incubated.

The Effects of Diets.

One of the characteristics of life in a densely crowded cage is that each of the surviving hoppers probably eats several of its fellows, or at least several exuviae during its development. It is conceivable that this may encourage the production of the *gregaria* characters, for if the locustine theory is correct, the amount of locustine in the body may be increased by the animal diet. Uvarov (1928) quotes the unsuccessful attempts of Nikolsky to breed *L. migratoria* on animal food, and Plotnikov (1924) found that hoppers of this species did not retain their *gregaria* characters if reared in isolation and supplied with freshly killed locusts.

Hoppers of *L. pardalina* were supplied with animal food in the following experiments :—

A. Fed on freshly killed locusts exclusively.

(1) One first instar *solitaria*, reared to fifth, grey with red and black spots, *solitaria* type.

(2) One first instar *gregaria*, reared to fourth, reddish-brown with black markings, *solitaria* type.

B. Fed on freshly killed locust daily, plus small quantity of green grass every two or three days.

(1) Four first instar *solitaria*, reared to fifth, all of the *solitaria* type, three of the hoppers showing reddish markings.

(2) Four first instar *gregaria*, reared to fifth, all of the *solitaria* type, one with orange and another with reddish markings.

In addition, attempts were made to rear five other hoppers on a diet consisting exclusively of locusts, and three more were tried on locusts plus grass, but all of these died in 2 to 13 days.

These results show that a diet consisting largely, or even exclusively, of other locusts was not sufficient to cause the retention or development of *gregaria* characters. Some of these hoppers had an unusual appearance, owing to the reddish coloration which is rarely found in *solitaria* types, indicating that the diet exerted some influence on the coloration and suggesting the possibility that cannibalism may be a factor contributing to the production of locustine.

A diet of green lucerne plus occasional bits of green grass was tried on two hoppers of the first instar *gregaria* type ; both survived to the fifth instar, and were described as light-grey and grey-brown *solitaria* types. Lucerne is not eaten by *L. pardalina* if graminaceous food is available.

The Hypothesis that Mendelian Inheritance is the Cause of Differences in Coloration.

Potgieter (1929) interpreted the differences in coloration observed in *L. pardalina* as being due to inheritance of colour types according to the laws of Mendel. Although he regarded this hypothesis as new, a very similar theory had been postulated by Plotnikov in 1927. Potgieter uses the term " brown " as the equivalent of what is described in the present paper as *gregaria* in the adult stage, and states definitely that the brown adult is derived from a hopper that is orange and black ; the " brown " of Potgieter is therefore the equivalent of the phase *gregaria* of the writer. Important points in this hypothesis are : (1) that *gregaria* mated with *gregaria* will produce almost all *gregaria*, with a rare occurrence of grey or green individuals ; (2) that *gregaria* by green or grey will always result in a majority of *gregaria* ; (3) that crosses between non-*gregaria* and non-*gregaria* could never produce *gregaria* offspring Evidently, then, the *gregaria* type must be dominant, although this is not definitely stated in these terms.

The author selected the types used in matings in the fifth instar, because the correct colour of the types used could best be determined in that stage of development. He reported the results obtained from a number of matings, but did not give details

of the density of the population in the cages. In all probability he reared the progeny of one pair collectively in a cage, in which case he could not have eliminated the factor of crowding.

In order to test this hypothesis, the writer selected from the material available in the cages a number of hoppers of the fifth instar typical of the phases *gregaria* and *solitaria*, of *L. pardalina*, and mated them together for the crosses listed in Tables XXI to XXIV. The progeny were reared partly in isolation and partly in small crowds, but the results of the two methods of rearing were noted separately. The cages used in each case are indicated in the tables: gauze cylinders refers to the type of cage figured on Pl. xxxviii, fig. 200; celluloid cylinders were those used in the work on green hoppers (fig. 202); for the crowds three types of cages are listed: A means one half of an incubator cage (fig. 197); B was one half of a cage 18in. by 18in. by 15in. (fig. 191), and C refers to a gauze cylinder (fig. 200). The eggs were placed in an incubator at about 31°C., in order to produce a prompt and even hatching.

TABLE XXI.

F_1 generation. Cross: *gregaria* type ♀ × *gregaria* type ♂.

Results obtained from six females, each mated to a different male.

L.p. number	Egg packages		Number of hoppers hatched (approx.)	Hoppers isolated in gauze cylinders: number that survived to 4th or 5th instar	Hoppers crowded			
	laid	incubated			Kind of cage	Number that survived to 4th or 5th instar		
						sol.	*trans.*	*greg.*
303	6	6	68	18 *solitaria*	A	0	1	33
305	3	3	0	—	—	—	—	—
352	5	5	124	1 *gregaria* ... / 1 *transiens* ... / 42 *solitaria* ...	A	0	3	7
353	5	5	60	10 *solitaria*	B	5	8	19
354	4	4	60	17 *solitaria*	A	0	4	23
355	5	5	100	24 *solitaria*	A	0	0	39
Totals ...	28	28	412	1 *gregaria* / 1 *transiens* / 111 *solitaria*		5	16	121

L.p. 352: The one hopper described as a *gregaria* type in the fifth instar had been in a cage with about ten others for about two weeks, and had become a second instar *gregaria* type before it was isolated.

L.p. 354: One of the 17 isolated hoppers was green in the fourth instar; this is one of the few hoppers reared in grey gauze cylinders that took on a green coloration. The great majority showed a dark bluish grey colour that harmonized very well with the gauze of the cages.

Out of the total hatch of 412 hoppers, 255 were reared to the fourth, fifth or adult stage, *i.e.*, about 61 per cent.

TABLE XXII.

F_1 generation. Cross: *solitaria* type ♀ × *solitaria* type ♂.

Results obtained from 10 females, each mated to a different male.

L.p. number	Egg packages: laid	Egg packages: incubated	Number of hoppers hatched (approx.)	Hoppers isolated in gauze cylinders: number that survived to 4th or 5th instar	Hoppers crowded: Kind of cage	Hoppers crowded: Number that survived to 4th or 5th instar: *sol.*	*trans.*	*greg.*
293	11	11	103	23 *solitaria*	A	0	4	28
315	8	8	44	22 *solitaria*		—	—	—
316	4	4	71	16 *solitaria*			*all died*	
416	2	2	28	8 *solitaria*	A	5	0	0
417	4	4	61	14 *solitaria*	C	6	1	2
418	7	7	68	8 *solitaria*	A	0	0	24
				Hoppers isolated in celluloid cylinders over growing grass: number that survived to 4th or 5th instar				
419	3	3	4	1 grey *solitaria* 1 green *solitaria*				
420	3	3	22	3 grey *solitaria* 3 green *solitaria*				
603	4	4	0	—				
671	7	7	30	7 grey *solitaria* 7 green *solitaria*				
Totals ...	53	53	431	113 *solitaria*		11	5	54

The females and males of Nos. 416, 417, 418, 419 and 420 were all green hoppers in the fifth instar, sent in from the field. The progeny of Nos. 416, 417 and 418, reared in isolation in gauze cylinders (30 hoppers), were all non-green solitary types, *i.e.*, grey to grey-black. Only in the case of the progeny of Nos. 419 and 420, kept on growing grass under celluloid cylinders, were green hoppers obtained in the proportion of 50 per cent. to 50 per cent. grey.

In Nos. 603 and 671 the parents, both male and female, had been reared in celluloid over growing grass and had not taken on a green colour. Of No. 603 no progeny were obtained; of No. 671 fourteen hoppers were successfully reared in celluloid over growing grass, and here also 50 per cent. became green and 50 per cent. grey.

Out of the total hatch of 431 hoppers, 173 were reared to the fourth, fifth or adult stage, *i.e.*, about 40 per cent.

TABLE XXIII.

F_1 generation. Cross : *gregaria* type × *solitaria* type.
Results obtained from 9 females, each mated to a different male.

L.p. number	Egg packages: laid	Egg packages: incubated	Number of hoppers hatched (approx.)	Hoppers isolated in gauze cylinders : number that survived to 4th or 5th instar	Hoppers crowded: Kind of cage	Hoppers crowded: Number that survived to 4th or 5th instar: *sol.*	*trans.*	*greg.*
(1) *gregaria* ♂ × *solitaria* ♀								
306	2	2	0					
693	4	4	6	0				
694	0	—	—	—				
695	0	—	—	—				
(2) *gregaria* ♀ × *solitaria* ♂								
307	2	2	24	7 *solitaria*				
356	7	7	90	31 *solitaria*	B	11	1	1
696	6	6	61	27 *solitaria*				
697	6	6	90	15 *solitaria*				
698	5	3	70	10 *solitaria*				
Totals ...	32	30	341	90 *solitaria*		11	1	1

The parents used in groups (1) and (2) above came from similar stocks, and parents and eggs were treated in the same way in both cases ; possibly the failure to obtain progeny in group (1) may have been due to the fact that the *gregaria* males were too large to copulate effectively with the small *solitaria* females.

Out of the total hatch of 341 hoppers, 103 were reared to the fourth, fifth or adult stage, *i.e.*, about 30 per cent.

TABLE XXIV.

F_2 generation of *gregaria* type × *gregaria* type.

The parents were phenotypically *solitaria* types in the 5th instar, having been taken from the isolated progeny of L.p. 352 and L.p. 354, all but two of which were of the *solitaria* type, as shown in Table XXI.
Results obtained from 7 females, each mated to a different male ; the eggs of only 3 pairs were incubated.

L.p. number	Egg packages: laid	Egg packages: incubated	Number of hoppers hatched (approx.)	Hoppers isolated in gauze cylinders : number that survived to 4th or 5th instar	Hoppers crowded: Kind of cage	Hoppers crowded: Numbers that survived to 4th or 5th instar: *sol.*	*trans.*	*greg.*
(1) Progeny of pair L.p. 352								
566	7	7	65	35 *solitaria*	B	0	2	10
567	7	0	—	—		—	—	—
568	10	9	40	16 *solitaria*	C	0	2	4
(2) Progeny of pair L.p. 354								
681	4	0						
682	5	0						
683	6	0						
684	4	4	8	—		—	—	—
Totals ...	43	20	113	51 *solitaria*		0	4	14

Out of the total hatch of 113 hoppers, 69 were reared to the fourth, fifth or adult stage, *i.e.*, about 61 per cent.

In addition to those listed in Tables XXI to XXIV, there were two other crosses :

(1) A male and female of the *transiens* type were mated together : 25 hoppers hatched and these were isolated ; 20 surviving to the fourth or fifth instar were all described as *solitaria* types.

(2) For the F_2 generation one of the isolated female progeny of the pair L.p. 352 (Table XXI) was mated with a *gregaria* type male ; this male came from a cage containing a large crowd, and was not related to the matings under discussion. The female was phenotypically of *solitaria* appearance, but being the daughter of a pair of *gregaria* adults she has to be described for our present purpose as genotypically a *gregaria* type. This was therefore a back-cross to the *gregaria* type ; it was known under the number L.p.569. Out of 55 hoppers that hatched 7 were reared in isolation to the fourth or fifth instars, and all 7 were described as *solitaria*.

Summary and Conclusions.

Adding together all the hoppers listed above, we find that 637 individuals were reared in these experiments from 34 different pairs of adults ; 394 were reared in complete isolation, and 243 under crowded conditions, but each crowd consisted of the progeny of one pair only. The majority of those isolated were placed in isolation on the day of hatching, but some first lived in a crowd for a week or two before being used to replace isolated individuals that had died.

Comparing the results in Tables XXI and XXII, we noted that the isolated hoppers acquired the *solitaria* characters, while those crowded tended to develop the *gregaria* characters, regardless of whether the parents had been *gregaria* or *solitaria*. Only two isolated hoppers from the pair L.p.352 showed *gregaria* characters, and one of these had lived in a crowd and had acquired *gregaria* characters before it was placed in isolation in its second instar. Table XXIII shows that crosses between *gregaria* and *solitaria* gave the same results.

In the second generation (Table XXIV) the progeny of the P_1 *gregaria* pair 352 reacted to isolation and crowding in the same way as all other hoppers, and the same was true of the F_2 back-cross to *gregaria* (L.p.569).

Examining the hypothesis of Potgieter in the light of these experiments, we find that the data presented in Tables XXI to XXIV are in direct contradiction with the three phases enumerated above. Instead of giving a majority of *gregaria*, the matings of *gregaria* by *gregaria* produced both *gregaria* and *solitaria* according to the conditions under which the progeny were reared. According to the second thesis, the crossing of *solitaria* and *gregaria* should always result in a majority of *gregaria*, but Table XXIII shows that 90 isolated hoppers all became *solitaria*. Thirdly, the mating of *solitaria* with *solitaria* is supposed never to produce *gregaria* progeny ; Table XXII shows that the progeny of these crosses developed *gregaria* characters when crowded and *solitaria* when isolated.

It is conceivable that heredity may play a part in determining whether a particular hopper is able to become green or not when reared under suitable conditions in isolation, and the experiments on the albino race of *L. pardalina* show that pure bred albinos completely lack the power to acquire the *gregaria* characters. But the hypothesis of Potgieter supposes that the acquisition of *gregaria* characters is determined by heredity in the non-albino, ordinary stocks of *L. pardalina* regardless of the environmental conditions. The data presented in the present paper emphasize the supreme importance of the environment in the determination of types of coloration and morphological characters. If colour types are due to heredity in these

TABLE XXV.

Locustana pardalina: Parents and F_1 progeny of single pairs, isolated and crowded in cages. Averages and ratios of biometrical data. Measurements in mm., to 0·1 mm.

L.P. number.	Description and method of rearing.	Number measured.	A	A/W	A/F	M/T	H/T	W	F	H	M	T
Males.												
352	Parent, in crowd	1	40·6	4·366	2·030	·7922	1·013	9·3	20·0	7·8	6·1	7·7
352	Progeny { in isolation	4	26·65	5·052	1·942	·8656	1·135	5·28	13·72	5·28	4·02	4·65
352	Progeny { in crowd	4	37·50	5·017	1·974	·8314	1·111	7·48	19·00	7·25	5·42	6·52
293	Parent, in isolation	1	29·6	5·103	1·922	·9038	1·135	5·8	15·4	5·9	4·7	5·2
293	Progeny { in isolation	6	23·62	4·869	1·905	·8626	1·141	4·85	12·40	4·98	3·77	4·37
293	Progeny { in crowd	11	30·73	4·788	1·963	·8242	1·084	6·42	15·65	6·11	4·64	5·64
Females.												
352	Parent, in crowd	1	42·5	4·942	2·104	·8250	1·075	8·6	20·2	8·6	6·6	8·0
352	Progeny { in isolation	4	30·25	5·426	2·047	·8591	1·091	5·58	14·78	6·00	4·72	5·50
352B	Progeny { in crowd	6	40·10	5·359	2·017	·8598	1·096	7·48	19·88	7·82	6·13	7·13
293	Parent, in isolation	1	—	—	—	·8906	1·125	7·3	18·2	7·2	5·7	6·4
293	Progeny { in isolation	1	30·4	5·527	2·000	·8421	1·105	5·5	15·2	6·3	4·8	5·7
8 293	Progeny { in crowd	7	33·83	5.333	2·086	·8360	1·067	6·34	16·21	6·60	5·17	6.19

insects, its influence is completely obscured by conditions of the environment. Studies of heredity in migratory locusts should therefore be designed in such a way as to eliminate the environmental factors, or at least to make due allowance for their effects.

The far-reaching effects of rearing in isolation and under crowded conditions are graphically shown by the photograph reproduced on Plate xxiii. Figs. 93 and 94 are the parents (L.p.352, Table XXI), and the two rows of locusts below them are their progeny; figs. 95-99 are locusts reared in isolation and figs. 100-104 are individuals reared together in a crowd. These specimens were photographed simultaneously on one plate.

Biometrical Comparisons of the isolated and crowded Progeny of individual Pairs of *L. pardalina*.

In Tables XXI to XXIV, the effects of isolation and crowding on the progeny of selected pairs of *L. pardalina* were judged on the basis of the coloration of the hoppers. Similar effects can also be detected in biometrical data based on measurements of the adults. One of the pairs listed in Table XXI, L.p., 352, was selected for measurement (see also Pl. xxiii), of a pair of *gregaria* × *gregaria* and some of their progeny. For *solitaria* × *solitaria* L.p. 293 was used (see Table XXII).

Table XXV presents the averages and ratios obtained by measuring the parents and part of the progeny of the two pairs 352 and 293. The data were obtained by the same methods as those described above (in connection with Table IV, p. 311). In comparing them with the figures for extreme *solitaria* and extreme *gregaria* in Tables IV and V, it is evident that the isolated progeny showed a distinct tendency to vary in the direction of the *solitaria* characters, while the crowded progeny tended to vary in the opposite direction. Counting the ratios only, and considering the variations to be " correct " if they were in the direction of *solitaria* for isolated progeny, and towards *gregaria* for crowded progeny, and " wrong " if they showed a tendency in the opposite directions, we may tabulate the results in this way :—

L.p.352. Male sex gave " correct " variations for both isolated and crowded progeny in 4 ratios ; female sex gave " correct " for both isolated and crowded in one ratio and " wrong " in three ratios.

L.p.293. Both male and female sex gave " correct " variations in all four ratios.

The Distribution and Breeding Grounds of *L. pardalina*.

The purpose of this publication is to discuss breeding experiments carried out in cages, rather than field observations, but it is desirable to supplement the discussion of cage experiments with a brief general account of conditions as they exist in the field. This account is based on (1) the official published reports of the South African Central Locust Bureau and those of the Union Department of Agriculture ; (2) informal discussions with Dr. T. J. Naudé and Mr. S. J. S. Marais about their observations on the distribution of the solitary phase ; and (3) personal impressions. The writer's impressions have been gained from observations made in the field between 1915 and 1917, when administrative locust duties took him into the field, and from brief vacation trips undertaken at various times between 1928 and 1931 with the assistance of the Union Department of Agriculture.

At the outset it should be clearly understood that the writer accepts the theory of phases as a fully established set of scientific facts in so far as it applies to the four species of migratory locusts occurring in South Africa. He is convinced that the progeny of one pair of the phase *solitaria* could multiply into a swarm of the phase *gregaria* under suitable conditions, and that an extensive invasion by swarms of the latter could literally arise from such small beginnings.

In discussing the distribution of this—or any other—species of migratory locust, it is necessary to distinguish clearly between three kinds of areas. First, there is the *range of invasion*: the whole geographical area subject to invasion by swarms of flyers, which usually leads to infestation by swarms of hoppers. Then we have the *permanent habitat*, which is included in the range of invasion, and could be defined as the area in which the species permanently exists in its phase *solitaria*. Finally, we must recognize the *areas of incipient swarming*; these obviously form part of the permanent habitat, and consist of localities in which scattered individuals of the phase *solitaria* have definitely been known to congregate into incipient swarms.

The Range of Invasion.

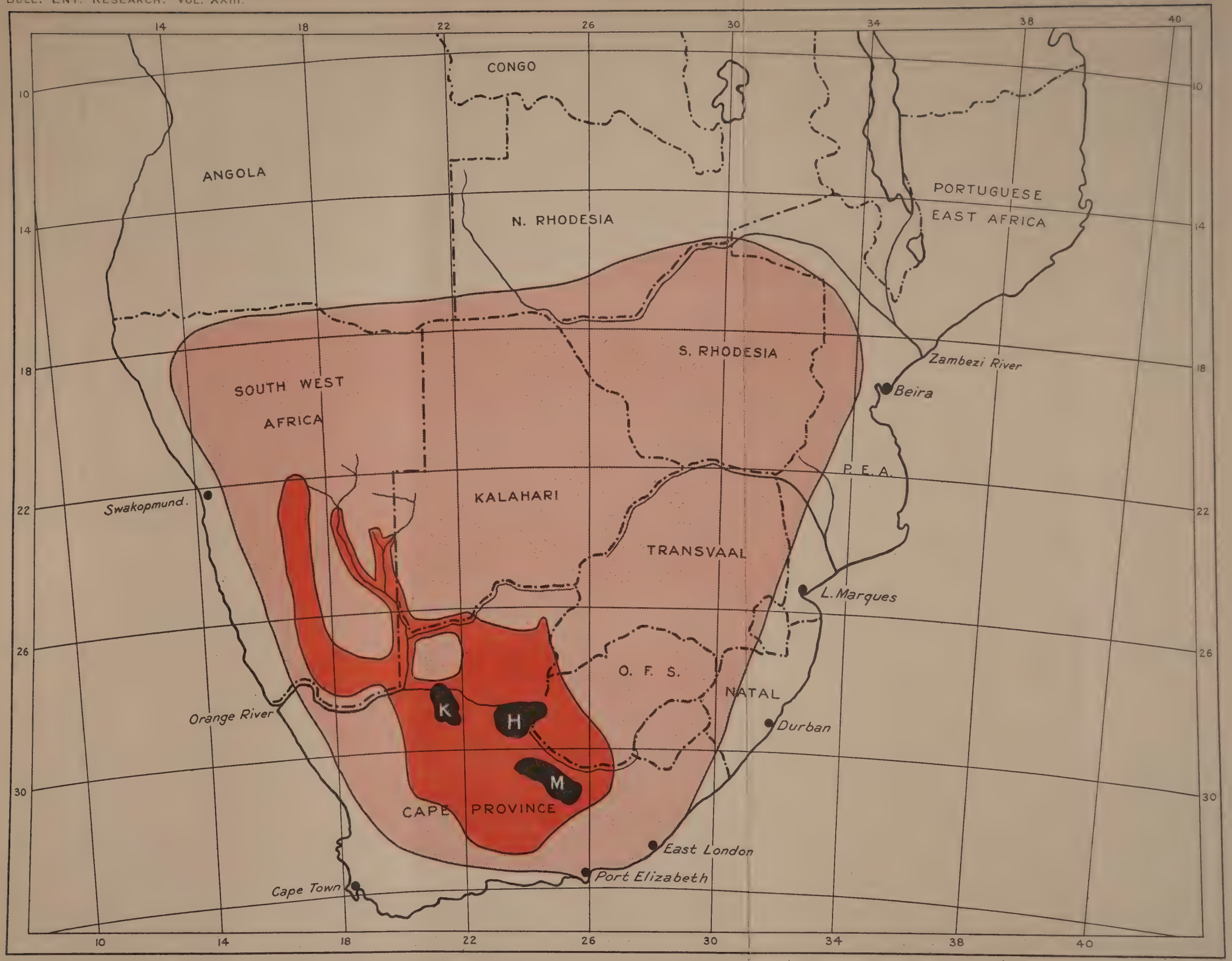
Without going into details, the recent history of this species may be briefly summarized by stating that there have been four distinct periods of invasion by swarms during the last forty years. The first came to an end in the season 1909–1910. Then there was an interval of freedom from swarms until 1913–14, when the second invasion began which reached its maximum in 1917–18. Two swarm-free seasons followed, but in 1920–21 the third and worst invasion commenced, and it continued until 1926. After a brief interval of one season, which was interpreted by some optimists as proof of complete extermination, incipient swarms once more made their appearance in the summer of 1927–28, and the campaign against these is still in progress in 1931–32.

The accompanying map shows the approximate limits of the area of invasion as it is defined in the official reports mentioned above. The exact limits are not known, because many of the invaded areas, such as parts of South West Africa, Bechuanaland Protectorate and Portuguese East Africa, are very sparsely if at all inhabited by Europeans. At the height of its periods of maximum abundance, the brown locust has in the past spread over practically the whole of Southern Africa from the Zambesi River to the south-eastern seaboard. Only the more humid eastern coast belt, the western desert seaboard and the south-western Cape Province have escaped invasion by its large flying swarms. The whole of this area of invasion was of course not heavily infested by swarms at any one time, and some districts, such as those in the mountains of Basutoland, are included in it although they may never have been visited by swarms.

Under the heading "brown swarm locust" Brain (1929) quotes certain historical references to locusts which devastated crops in the earliest years of European settlement in the south-western Cape Province. It seems very improbable that these swarms could have been of the species *L. pardalina*: (1) we have no record of an invasion of the western Cape Province by *L. pardalina*; (2) swarms of the red locust *N. septemfasciata* invaded the Cape Peninsula in 1843 and reached as far west as Swellendam in 1896.

Many different types of vegetation are included in the invasion area, covering as it does the Karroo semi-desert, the Kalahari thorn country, the highveld grassland and the eastern tree savanna. In its phase *gregaria* the species breeds, temporarily at least, in country that differs very widely from the semi-desert Karroo where its permanent habitat lies. The occurrence of swarms in the eastern agricultural areas is a matter of grave national concern, but this type of country is not by any means the natural home of the species, for in spite of recent invasions by swarms, the phase *solitaria* does not appear to be able to maintain itself in the eastern grasslands. Furthermore, it is very doubtful whether even the swarms could continue to maintain themselves for an indefinite period in the eastern highveld of the Transvaal and Orange Free State, or in the tree savanna (bushveld) of the Transvaal, where there is a dense growth of tall grasses.

The writer is convinced that the invasions of the grassveld areas of the northern Kalahari, the eastern Orange Free State, the Transvaal and Southern Rhodesia have



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LOCUSTANA PARDALINA (Walker)

The range of invasion 1906 - 1926.

The permanent habitat of the ph. solitaria 1915 - 1931.

Destruction of incipient swarms arising from congregating ph. solitaria 1928 - 1931.

originated in the past from swarms migrating out of the areas bearing the Karroo type of semi-desert vegetation.

Potgieter (1929) stated that " the whole area in which locusts have bred in the past should be considered as one large natural breeding ground." This conclusion was arrived at largely because " typical so-called solitary flyers " had been found in parts where the conditions of soil and vegetation did not agree with the description given by the present writer (Faure 1923) of the areas in which the phase *solitaria* appeared to find its natural home. Seven localities were mentioned by Potgieter ; five of these are in South West Africa, in districts covered largely by the Karroo type of vegetation and therefore potentially part of the natural home of the species. The two other localities are in the Transvaal and Orange Free State respectively, in eastern grassveld. But the occurrence of isolated locusts of the phase *solitaria* in the eastern grassveld during the years 1924 and 1925 probably only meant that a small number of individuals had survived for one or two seasons after the invasion by swarms of the phase *gregaria*, because practically the whole country was overrun by swarms between 1922 and 1926. Potgieter's conclusion that " the idea of a temporary and permanent breeding ground ascribed to the brown locust is untenable " was based on inadequate grounds and does not call for further comment.

The Grassveld as a Breeding Ground.

In January 1928, about three years after the last invasion by swarms, the writer made a hurried search through certain parts of the north-western Transvaal in order to try to find *L. pardalina* in areas that had been severely infested. From Pretoria the route lay north-west through parts of Waterberg, then south again through the Rustenberg and Marico districts to Lobatsi, and then south to Mafeking and Vryburg in the Cape Province. About two weeks were spent between Pretoria and Vryburg on this trip. It was admittedly a hurried inspection, but walks of a quarter mile to a mile or more were taken about every 20 to 30 miles, and in some places every 10 miles. Not one grasshopper was seen in the Transvaal that could even have been mistaken for *L. pardalina*, but as soon as we came on to the Karroo-type patches of the Vryburg district (*e.g.*, on Armoedsvlakte) and further south in Taungs, single individuals of the phase *solitaria* were found without any more extended collecting than what we had done in the Transvaal. These observations indicate that the species was very rare during the summer of 1927–28 in the Transvaal on some of the farms that had been heavily infested by swarms between 1922 and 1926.

Further very significant evidence bearing on the origin of invasions and the status of the grass veld as a breeding ground is to be found in the records of the destruction of swarms during the past eighteen years. After the big outbreaks of 1906–1909, during which the Transvaal and Southern Rhodesia were heavily infested, there was a brief respite, but when the trouble recommenced during 1913–14, the new infestation had to be combated in the Middelburg area of the Cape Province, *i.e.*, in the Karroo country. All the campaigns carried on during the period 1914–1917 were centred in the south-western Orange Free State and adjoining districts of the Cape, which are largely of the Karroo type.

Similarly, after the very severe invasions of 1922–26, the recrudescence of incipient swarming began in 1927–28 in Hope Town, Herbert and adjoining parts of the Karroo country, while no locusts have been reported since 1926 from grassveld areas, such as those of the Transvaal, Bechuanaland, or Rhodesia. Not only have no locusts been reported from the grassveld areas, but while the Karroo country around Hope Town was heavily infested with scattered flyers in 1928, an entomological expedition was specially sent into the northern grassveld of the Kalahari to study conditions in the parts which had served as breeding grounds in 1922–26, and it returned after a month's trip without having seen one single specimen of *L. pardalina*.

These observations admittedly do not establish the case completely, for parts of the Kalahari are to a large extent *terra incognita*, but evidence is gradually accumulating to show that the northern Kalahari and other grassveld areas only serve as temporary breeding grounds for swarms which have migrated into them from the permanent habitat which lies elsewhere.

The Permanent Habitat.

In dealing with locusts, one should guard against the danger of being so fully occupied with the swarms as to lose sight of the scattered individuals of the solitary phase. Especially when they begin to congregate into the loose aggregations known as incipient swarms, these scattered individuals are of far more importance, from the ecological standpoint, than the large swarms of *gregaria*. The natural home or permanent habitat of a migratory locust is the area in which it finds conditions suitable for existence as a solitary grasshopper, and from which it is presumably never entirely absent.

L. pardalina is in its solitary state a lover of wide open spaces in which it can fly off suddenly, unhampered by tall densely growing grass, and settle down again on a bare patch of earth. It is a typically geophilous grasshopper, differing in this respect from *Nomadacris septemfasciata*, which appears to be strongly phytophilous. In habits the solitary forms of *L. pardalina* are very similar to the very common *Sphingonotus scabriusculus*, Stål, a grasshopper with broad black and blue bands on its underwings, but the former are stronger flyers. Although exact data are not available, it seems safe to assume that the phase *solitaria* of *L. pardalina* is exclusively a grass feeder in the field, although Karroo bushes (*Pentzia*, *et al.*) are a characteristic feature of its permanent habitat.

Systematic field observations have not yet been carried out sufficiently to warrant final conclusions, but the writer believes that the permanent habitat of *L. pardalina* will ultimately be proved to consist of veld characterized more or less as follows: (1) vegetation: scattered shrublets of the Karroo-bush type, with dwarfed grass that usually grows in tufts not more than an inch or two in height; (2) soil: stony, shallow, hard, usually lime-stone (calcrete) but also other formations; (3) climate: semi-desert, subject to droughts.

The type of veld on which *L. pardalina* ph. *solitaria* is most readily found during periods of minimum abundance in districts like Hope Town, Herbert and Jacobsdal, is the flat expanse of hard, shallow soil on which the underlying calcrete lies exposed on the surface in the form of white lime-stone pebbles (Pl. xxiv, fig. 106). This lime-veld occurs in the Hope Town area in stretches that may be less than a mile or many miles wide, alternating with slightly raised " bulte " of reddish Kalahari blown sand (figs. 105 and 108). In the writer's limited experience it is a rare occurrence to find *solitaria* in the grass on the red sand in this type of country, although it may be quite common on the adjacent lime-veld. As soon as the numbers increase sufficiently for incipient swarms to be formed, the adults congregate for oviposition on the sandy soil. It does not seem possible, in view of the distribution of the nymphs, that the *solitaria* females could also habitually select sandy soil for egg-laying; if they do not, we have here an interesting difference in the behaviour of isolated and crowded individuals.

In other districts of the Karroo, such as Beaufort West, the typical calcrete-pebble veld is not so much in evidence, but the *Pentzia*-plus-grass vegetation is present in approximately the same density of growth on shales and other formations, and some of these areas appear to be equally suitable for permanent colonization by the phase *solitaria* (fig. 107).

On the map the area labelled " permanent habitat " is an approximate delimitation of the region in which the phase *solitaria* has repeatedly been found during the

past seventeen years by entomologists and locust officers, on the types of veld described above. The phase *solitaria* has occasionally been found outside this area; in some cases, such as Potgieter's record (1929) for Pilgrim's Rest, Transvaal, in 1924, this was undoubtedly a temporary condition due to recent visitation by swarms; in other cases the finds may denote permanent colonization. The writer would place in the latter class some interesting observations kindly communicated to him by Mr. G. van Son of the Transvaal Museum, who took part in the Vernay-Lang Kalahari Expedition in 1930. Typical examples of the phase *solitaria* were taken in small numbers by Mr. van Son at Gemsbokpan, near Ghanzi, and at Kaotwepan, in both cases on limestone formations bearing small shrublets similar to the Karroo bushes in appearance. Many weeks were spent collecting on the sand veld of which the Kalahari largely consists, but *L. pardalina* was never observed except on the two pans.

Comparing this known area of permanent habitation with the vegetation map of Pole Evans (1930), we note that it falls very largely in the zone of the Karroo semi-desert vegetation, and includes smaller portions of the Kalahari thorn-veld and Namaqualand coastal desert. The Kalahari thorn-veld of Pole Evans includes patches of Karroo-type veld along the dry beds of water-courses such as the Molopo, Kuruman and Nossop, and also on the edges of scattered pans. In districts like Herbert and Hay, which fall entirely in the Kalahari thorn-veld, there are extensive stretches of lime-veld resembling that of Hope Town very closely in general appearance. The inclusion of parts of the Kalahari thorn country in our permanent habitat of *L. pardalina* is due to these included lime-veld portions and should not be interpreted to mean that the whole of the vast Kalahari sand-veld region is suited to the phase *solitaria*.

Other Acrididae associated with *L. pardalina*.

The other ACRIDIDAE associated with the phase *solitaria* have not received much attention. The writer regards *Sphingonotus scabriusculus*, Stal, as the grasshopper most frequently found on the patches where *L. pardalina* also occurs under conditions of minimum abundance; in other words, the two forms appear to have more or less the same ecological requirements. Other forms of the subfamily OEDIPODINAE, commonly seen in the permanent habitat, may be briefly mentioned: *Oedaleus nigrofasciatus*, DeGeer [=*gracilis*] has a much wider distribution eastwards and northwards and frequently occurs in a denser growth of grass; it is not a good indicator of the presence of *L. pardalina*, but deserves close study for various reasons, among others because its nymphs resemble those of *L. pardalina* rather closely. *Acrotylus* spp. are common, but appear to have a greater affinity for sandy places than *L. pardalina*, they also range much further afield and are not good indicators. *Scintharista magnifica*, Uvarov, is a striking form with red underwings that occurs with *L. pardalina*, but it is not common, and is more partial to slopes covered with large stones and boulders. Its nymphs might be mistaken for those of *L. pardalina*.

The Areas of incipient Swarming.

It is possible that the whole of the permanent habitat of *L. pardalina* may be potentially suitable for the rapid multiplication of numbers which leads to congregation into incipient swarms. But the particular combinations of favourable climatic conditions which make such increase possible may be of very rare occurrence in some of the drier regions. In the present unsatisfactory state of our knowledge, the only safe way to identify the areas of incipient swarming is to mark down as such the farms and portions of farms on which the process of congregation into swarms has actually been observed. From the strictly scientific point of view I doubt whether this process has ever been satisfactorily observed in the field through its initial stages. But the general evidence that swarms do arise in this way is so convincing that there is no reasonable ground for further doubt.

Before 1926 very little was done in the way of scouting to look for swarms in swarm-free years. One waited for farmers and police officers to report, and when the reports did perchance come in, the swarm formation had usually proceeded so far that it was very uncertain whether the swarms found had been begotten by other swarms or arisen out of congregating *solitaria*. The parts of the Kalahari that are to-day frequently traversed by scouting locust officers as a matter of routine were largely a closed book until the severe infestation of 1922–26 forced the Government to penetrate into the more accessible parts of the waterless regions in order to attempt the destruction of the swarms breeding in it. Incidentally, locust invasions have contributed largely to the penetration of portions of this vast region by civilization.

The writer is convinced that the outbreaks of 1915-17 in the western Orange Free State and adjoining parts of the Cape had their origin in the congregation of locusts of the phase *solitaria* and not in pre-existing swarms. But owing to the absence of any organized scouting in the years preceding these outbreaks, and the meagreness of our knowledge about the conditions " at the back of beyond " in the Kalahari, it is on the whole safer not to lay too much emphasis on the events of 1915-17 as evidence of the formation of swarms out of congregating *solitaria*. For these reasons, the whole of the south-western portion of the Orange Free State is not marked down on the accompanying map as an area of incipient swarming.

Since 1926 things have been different. Several senior locust officers were permanently employed on scouting after the invasion had come to an end ; therefore there is sound foundation for the statement that the recrudescence of trouble in 1928 was very largely, if not entirely, due to congregating *solitaria*. It is worth mentioning that these practical destroyers of the phase *gregaria* took little interest in the theory of phases until 1928 ; the rapidity of swarm formation " out of nothing " in 1928, and their experience in the destruction of incipient swarms between 1929 and 1931, have now completely convinced them that transformation of the phases takes place in the field.

In the last few years entomologists have also been doing field work on *L. pardalina*, therefore the general situation warrants the definite statement that a great deal of locust destruction has since 1928 been necessary to deal with congregating *solitaria* and their progeny. It will therefore be understood why the areas of incipient swarming, marked on the map, are only those definitely incriminated as such between 1928 and 1931. Three areas are drawn. The southern area, labelled M includes Middelburg, Steynsburg and De Aar. H represents Hope Town, Herbert and Jacobsdal, and is probably the most typical and the most dangerous area of the three. K lies largely in the district of Kenhardt, and is not so well known to entomologists as the other two. Near the northern boundary of the permanent habitat in South West Africa, swarm formation out of *solitaria* has also recently reported to have taken place on a small scale.

In these three areas, M, H and K, we have a large central block of the permanent habitat marked down as country that demands the eternal vigilance of the locust administration. In view of the fact that our reliable data cover the happenings of four summer seasons only, one fears that further experience may greatly increase the extent of the area known to be suitable for incipient swarming.

Prospects for the Future.

The general position at present is that there are sound reasons for optimism as to the possibilities of keeping *L. pardalina* under control to such an extent that the vast invasions of the past will not be repeated. This cheerful prospect rests mainly on two suppositions : (1) that the present vigilance and energetic destruction of incipient swarms will not be relaxed, but intensified and improved by research and experience ; (2) that the largely inaccessible northern sand-veld of the Kalahari is only of importance as an invasion area and does not come into consideration as part of the permanent

habitat or the areas of incipient swarming. Fortunately, most of the country known as permanent is occupied by Europeans and can be worked by motor transport. It is a vast area, and much of it very sparsely populated, so that efficient scouting for congregating solitary locusts may not prove completely practicable. But given better co-operation on the part of the farming community, there need be no danger that an incipient outbreak will escape official notice until it has assumed alarming proportions.

THE EMBRYONIC DIAPAUSE OF *L. PARDALINA*.

Incubation 5 to 37 Months after Oviposition.

It is well known that the eggs of *L. pardalina* lie dormant in dry soil for many months, and that they may be expected to hatch about ten days after the first rain in warm weather. In the laboratory this has repeatedly been proved to be the case: the eggs which have been laid in dry soil are kept dry for weeks or months, until it is convenient to hatch them. They may be stored at room temperature, and even the high temperature reached by the soil during hot summer weather will not injure them in their natural position in the packages. As soon as they are wetted and subjected to a favourable temperature, say, about 31 degrees C., development proceeds rapidly and hatching occurs in about a week.

C. P. Lounsbury (1910) reported that he had succeeded in hatching a few hoppers from eggs which had been stored dry for 3½ years. The eggs had been dug out about October 1904, and the last hatching occurred in May 1908, therefore their age was probably nearer 4 years than 3½, because eggs are usually laid from April to June. In 1923 I reported an unsuccessful attempt to hatch eggs which were about 5 years old.

In July 1928 many hundreds of egg packages were collected in the Herbert district of the Cape Province, and this material has been used in tests of the ability of eggs to survive long periods of drought. From February to April 1928, incipient swarms of the brown locust appeared on many farms in Herbert and adjoining districts, and scattered *solitaria* hoppers and adults were present in large numbers. In May and June these locusts congregated and laid their eggs in deposits in which the egg packages could readily be found in large numbers. They could therefore be described as eggs laid by swarms, but strictly speaking they were the eggs of locusts of the phases *solitaria* and *transiens* which had oviposited together in compact deposits. Many of the dead adults lying about in July were typically *solitaria* in appearance.

The locust administration endeavoured to reduce the numbers of the insects by dusting powdered arsenite of soda on the adults as they settled together for the night on the egg-laying grounds, and large numbers were killed in this way. Eggs were taken from two deposits; one on which arsenite had been dusted and another that had escaped this treatment. These eggs were kept apart and tested in parallel hatching experiments under identical conditions, but no differences could be detected, therefore no distinction is made between the two lots in Table XXVI.

The dry egg-packages were stored in cardboard boxes and tins for about two years at ordinary room temperature, and then they were placed in dry sand, some in tightly closed fruit jars and others in open jars. Comparative tests showed no difference in the percentage hatched from the lots stored in tightly closed and open containers.

For incubation the packages were placed in their natural upright position in clean sand in jars or tins, which were covered with mosquito netting or calico. The soil was thoroughly wetted, and the containers placed in an incubator running at a constant temperature of about 31°C., this temperature having been found by experience to give good results. When the sand looked dry, more water was added

from time to time. Comparative tests were made of different methods of incubation : some eggs were kept in the incubator day and night, except when removed for examination ; some were kept in the incubator at night and at room temperature for the day, and *vice versa* ; the majority were removed from the incubator and kept at room temperature for 3 to 4 hours every morning. No appreciable difference was found in the percentage of hatching or incubation periods required under the different conditions, therefore these details are omitted from Table XXVI.

In all cases where attempts were made to hatch eggs that were two years old or older, control tests were carried out simultaneously. That is to say, eggs laid two or three months before in cages were wetted and incubated at the same time as the older eggs and given the same treatment. The controls invariably produced a good hatch of hoppers.

TABLE XXVI.

Attempts to hatch eggs of *L. pardalina* collected in the Herbert district, Cape Province, in July 1928.

L.p.E. record number	Age of eggs, counting from 30.vi.1928		Total number of packages	Number of tests	Minimum incubation period in days	Total hoppers hatched	Average hatch per package
	years	months					
15b	—	5	30	1	9	600	20
17	—	6	10	1	10	150	15
27	1	—	13	1	10	208	16
28	1	3	15	1	8	345	23
31–34	1	7	86	4	10	1698	19·7
45–46	1	9	76	4	10	875	11·5
47–48	1	10	37	2	10	298	8
50–51	1	11	24	2	11	217	9
52, 60	2	—	36	2	11	110	3
62	2	1	17	1	11	132	8
64	2	2	190	1	9	500	2·6
70	2	4	140	1	8	513	3·6
71–72	2	5	70	2	10	127	1·8
73, 77	2	6	44	2	11	93	2·1
81	2	8	12	1	11	31	2·5
82–83	2	10	100	2	11	4	0·04
87–89	3	—	18	3	—	—	—
25–26) 91–93)	3	1	160	20	13	17	0·11

Summarizing the results in Table XXVI, we note that the maximum diapause observed was three years and one month. It is possible that some of the eggs which hatched after this long interval may have been a month older, because egg laying probably began in May of 1928, but in taking 30th June as the starting point, we may be certain that the eggs had been laid before that date. The percentage of eggs which hatched after three years was only about 2 to 4 per cent.

The hoppers which hatched three years and one month after the eggs had been laid were quite active and normal in appearance. They were placed in breeding cages and some of them were successfully reared to the adult stage, in which they had the general characters of the phase *solitaria*.

The figures in the column " average hatch per package " provide only a very rough approximation of the percentage which hatched, because the number of eggs in a package varies between wide limits, from 10 or less to 60 or 80. While the eggs were from 5 months to about two years old, they yielded a fair hatch, which varied from 3 to 20 hoppers per package. From two years onwards the number

hatching decreased greatly, and at three years the figures per package were as low as 0·04 and 0·11.

It was considered advisable to keep the packages as whole as possible in order to increase the chances of hatching. After incubation it is not easy to determine the exact number of eggs originally present in the packages, therefore the percentage hatching could not be accurately determined. In the tests of eggs five months to three years old no serious attempt was made to arrive at the percentage which hatched, but it was estimated to vary from about 25% to 50%. Twenty lots of packages 3 years and 1 month old were incubated, but a few hoppers hatched out of 5 lots only. The total number of eggs incubated was determined with a fair degree of accuracy in the case of these 37-months-old eggs, and from 2–4% was found to have hatched.

Incubation two Months after Oviposition.

Field officers who have had experience with *L. pardalina* know that two generations may be produced during one summer season under favourable conditions. Locusts hatching in October will be on the wing towards the end of November, and they may deposit eggs less than two months after the last moult. If rain falls on these eggs in January or February, a second generation of hoppers will appear.

During the breeding experiments two generations were obtained each summer for three successive seasons from the same stock of material without any difficulty. Eggs laid in the cages by crowds or by isolated individuals could be hatched at any convenient time from a week or two to a year or more after they had been laid, provided that they were kept dry in the interval.

The following records of two lots of eggs which were about two months old when incubated will serve as examples:

L.p. 255: 160 packages incubated 20.ii.1930, age about 60 days; first hatch on eighth day, 1,300 hoppers emerged, average per package 8.

L.p. 622: 133 packages incubated 6.ii.1931, age about 60 days; first hatch on eighth day, 717 hoppers emerged, average per package, 5·4.

Incubation immediately after Oviposition.

The question now arises, how soon after they are laid could the eggs hatch if the conditions were favourable?

The following notes on the incubation of eggs that were from 1 to 14 days old provide the answer:—

L.p.E. record number	Date placed in incubator	Maximum age of eggs in days	Number of packages	Minimum incubation period in days	Total hoppers hatched	Average hatch per package
75	9.i.31	1	3	16	6	—
74 ...	5.1.31	3	7	12	30	62·5
79 ...	23.i.31	7	4	12	35	70
78 ...	16.i.31	14	6	12	43	50

These eggs were kept in an incubator running at a temperature of 31°C., but were left out at room temperature for 3 to 4 hours daily. During these tests the incubator went out of order for a few days; this probably accounts for the minimum incubation period of 12 days as compared with the usual period of 8 to 10 days. The eggs were from cage L.p. 622, the F_5 crowded progeny of *solitaria* material from the field. They were laid in dry soil but were thoroughly wetted before they were placed in the incubator.

The eggs of *L. pardalina* will therefore hatch in 8 to 12 days at favourable temperatures as soon as they are wetted. If kept dry, the embryos will readily remain alive for a year or more, and a small percentage was even found to hatch more than three years after they had been laid. If the artificial "drought" is prolonged for more than four years the embryos all die. This remarkable embryonic diapause is a feature which apparently does not occur in any other species of migratory locust. It is a very great advantage to *L. pardalina* in its natural habitat, where the rainfall is scanty and very irregular.

The Stage of Development of the Embryo during Diapause.

The development of the embryo has not been studied in detail, but the following observations may be of interest. The egg is about 6 mm. in length and about 1·4 mm. in diameter at the middle. It is slightly curved, the concave side being on the ventral aspect. At the posterior pole there is a small cap-like area marked off by a circular depression which enables one to recognize this end without difficulty. Some hours after the eggs have been wetted, the chorion can be peeled off without rupturing the vitelline membrane.

Some eggs laid in dry soil in cages were kept dry and examined about six months after oviposition. In order to facilitate removal of the chorion the eggs were kept moist for about 24 hours, but they were first dropped into boiling water in order to kill the embryos. In these eggs the embryo was found to be large enough to see with the naked eye, and the segmentation and rudiments of appendages could be observed with the aid of a hand lens magnifying 10 diameters. It is white, partly clear and partly opaque, distinctly visible in the clear yellowish yolk if the egg is held against the light. The cephalic end of the embryo lies close to the posterior pole of the egg, and in side view is seen to be sunk into the yolk. The posterior end is at the surface of the yolk, and lies about 2·5 mm. from the posterior pole of the egg. The total length of the embryo is therefore about one-third of the length of the egg. Rudiments of thoracic appendages are visible, and the segmentation of the abdominal region is indicated on the lateral margins.

In another lot of dry eggs examined during diapause, the embryos were found to have the same general appearance, and to lie in the same inverted position, but they were longer, being a little more than half as long as the eggs. These eggs came from the field; they were laid during April and May, and were wetted by about ½in. of rain and snow during cold weather. When warm weather came in September, some of the eggs hatched, but many did not. Those remaining unhatched were tested in the incubator at 31°C. after wetting in November, and found to hatch after about 6 days. The eggs studied in this case were therefore also in a state of diapause, but their embryos were larger than those in the eggs laid in cages and kept dry for six months; the winter rain had wetted them, and a certain amount of additional development had been made possible by the early spring temperatures.

Other lots of eggs in a state of diapause have been examined from time to time, but in no case were embryos found in them larger than those described in the two preceding paragraphs.

It is evident that the early stages of embryonic development proceed up to a certain point without any assistance from external sources of water, and that the embryo is able to survive long periods of drought in the stage described above, in which it is about one-third to one-half as long as the egg. Furthermore, an increase in length from about one-third to about one-half the length of the egg may take place, if moisture is available at temperatures that are not sufficient to complete the development. After this increase in length, the embryo returns to a state of diapause.

Hatching delayed in spite of favourable Conditions.

There is a popular belief that the eggs of *L. pardalina* sometimes lie over in the soil for long periods, even up to twenty years, in spite of rain and warmth. This may be dismissed as a myth so far as the vast majority of eggs are concerned, but curiously enough, certain laboratory results show that there may at least be a grain of truth in this popular superstition : a small percentage of the embryos were found to lie dormant, alive, through several incubations under the most favourable conditions known.

Table XXVII contains the records of four lots of eggs laid in cages by the locusts bred in the cage L.p. 138 (see Table I, p. 303). About 50% of these locusts had a *gregaria* type of coloration in the fourth and fifth instars, so the group may be said to have been of the *transiens* type ; the adults were isolated for egg-laying.

The eggs were wetted and incubated in the usual way during February 1929 ; after the first batch of hoppers had emerged the sand was re-wetted and the jar replaced in the incubator, with the result that more hoppers appeared a week or two after the first lot, and this process was repeated two or three times. Our usual experience was that the hatch which occurred on the 8th or 10th day was never a complete one, and that repeated wetting and incubation would produce more hoppers in rapidly decreasing numbers for some weeks.

The three double columns in Table XXVII are labelled first, second and third incubation periods ; this means that each " period " consisted of several wettings and incubations over a period of some weeks.

TABLE XXVII.

Delayed hatching of eggs : *L. pardalina.*

L.p.E. number	Number of packages	First incubation period : 13.ii.29–5. iv. 29		Second incubation period : 4–20. iv. 30 *i.e.*, 13 months after first		Third incubation period : 1–24. x. 30 *i.e.*, 19 months after first	
		First hatch, number of days after 13.ii.29	Total hoppers hatched	First hatch, number of days after 4.iv.30	Total hoppers hatched	First hatch, number of days after 1.i.30	Total hoppers hatched
20 ...	40	8	346	10	23	*not attempted*	
21 ...	41	8	281	10	39	8	11
22 ...	36	8	318	—	0	9	23
23 ...	42	8	365	9	1	11	25

L.p.E. number	Number of packages	Original total number of eggs (approximate)	Approx. percentage of original total hatching after second incubation	Approx. percentage of original total hatching after third incubation
20	40	500	5	—
21	41	500	8	2
22	36	500	—	5
23	42	500	0·2	5

After the first incubation period, which lasted from 13th February to 5th April, 1929, the egg jars were put aside in a cupboard for later examination and left there for about a year. Then it was noticed that the jars contained a number of eggs which appeared to be quite sound, and after re-wetting and incubation a delayed hatch amounting to about 5% of the original total was obtained. A second delayed

hatch was obtained during the third period, about 19 months after the original incubation.

The hoppers which hatched during the second and third periods of incubation were placed in cages, and about 20 individuals survived to the adult stage. From those of the second period, three were reared to the adult stage in the F_2 generation. This indicates that the insects emerging from these delayed hatchings were not lacking in vitality.

These results indicate that a small percentage of eggs may lie over for a year or more in the field even after several good rains have fallen on them during hot weather. If this does occur, it will be a great advantage to the species, in view of the vicissitudes of its existence resulting from the extremely spasmodic nature of the rainfall in many areas in which it exists permanently. It often happens in the drier areas that a light shower falls which is enough to cause the eggs of *L. pardalina* to hatch and to bring out a slight growth of green grass; if this is not followed by more rain the grass soon disappears and the hoppers may die of starvation. The lying over of some of the eggs would therefore greatly improve the chances of survival of the species in desert country.

A supposed Case of delayed Hatching on a large Scale in the Field.

On the farm Amandelpan, in the district of Hope Town, C.P., an extensive deposit of eggs was laid by the congregating locusts of the phases *transiens* and *solitaria* during May and June 1928. Powdered arsenite of soda was dusted on the locusts while egg-laying was in progress on this spot. After good rains had fallen, large swarms of hoppers hatched, and these were destroyed near the egg deposit, but it was noticed that a number of apparently sound eggs remained in the ground. The deposit was carefully watched for many months, but no subsequent hatching took place that attracted the attention of farmers and locust officers.

Some of these apparently sound eggs were dug out on Amandelpan in December 1928, about two months after the swarms of hoppers had been destroyed. Several lots were incubated under controlled conditions in the laboratory in January 1929, but not one hopper emerged from them. The eggs were discarded after several wettings and incubation for about a month. A possibility remains that a small percentage of these eggs might have hatched after a year or 18 months, as in the case of those listed in Table XXVII, but if any of the embryos had been alive one should have expected a few to hatch in January 1929, this being the second "period" of incubation.

The most acceptable explanation of this Amandelpan case appears to be that some of the poisoned females were able to lay eggs which failed to hatch. An analagous case was reported by Ransom and Graybill (1912) in the females of the tick, *Boophilus annulatus*, which had been dipped in arsenite of soda. A further point of interest in this connection is that the eggs in the dead bodies of poisoned females lying on the egg deposit were still yellowish in colour in December 1928, about seven months after the insects had been killed. This shows that the yolk is very durable, and may account for the sound appearance of the eggs which failed to hatch in the incubator.

AN ALBINO RACE FOUND IN *L. PARDALINA*.

In October 1929 we noticed three very pale, whitish-grey individuals in the large cage L.p. 255, containing about 8,000 to 9,000 hoppers. This crowd was bred in connection with the attempt to produce the phase *gregaria* out of the solitary phase. Similar pale individuals had occasionally been observed in incipient swarms in the field, but they were regarded as just one more of the endless variety of colour types

produced in the solitary phase. In the cage, these three were very conspicuous in a crowd that was very dark in colour, consisting almost entirely of *gregaria* hoppers of the second and third instars, and we therefore assumed that they must be albinos. For fear of their being injured or eaten, the three hoppers were removed to another cage.

Two were males and one was a female. The female and one male were kept together under the number L.p. 292. The other male was mated with *gregaria* and solitary type females (L.p. 324 and 330). The female 292 laid 8 packages of eggs; these were incubated and about 130 hoppers were obtained. In the first instar these were pale grey-speckled, resembling the first instar *solitaria* hopper very closely (Pl. xv, fig. 21). Fifty-one were reared to the fifth or adult stage in isolation, and thirteen in three small crowds; all the progeny that lived to the fifth or adult stage were albinos like their parents.

When inbred these albinos proved to be a pure line to the F_3 generation, as the following tabulation shows:—

P_1: 1 female laid 8 packages.
F_1: 103 hatched, 64 survived, all albinos.
P_2: 19 females laid 43 packages.
F_2: 209 hatched, 72 survived, all albinos.
P_3: 8 females laid 8 packages.
F_3: 34 hatched, 4 survived, all albinos.

"Survived" means that the insects reached the fourth or fifth instar, or that they became adults.

About ten of the F_2 adults were still alive in July 1931, and also two of the F_3 generation. The strain is not a vigorous one, for the numbers decreased rapidly, although the albinos were given the same care and attention as other stocks of *L. pardalina* that have thrived.

A typical example of a fifth instar albino is illustrated (Pl. xiv, fig. 4). There was some variation, some of the hoppers being lighter and others somewhat darker. The young adults were very pale, of a dirty white colour, but after about a week they usually became more or less greenish-yellow, and some were almost bright green, although their generally pale coloration would distinguish them from non-albino green adults. When the flyers were about a month old they were much darker than the young flyers; with age they developed a whitish grey colour which later turned to a light grey-brown. The males also showed a good deal of yellow similar to that which is characteristic of *gregaria* males at the time of mating and egg-laying (Pl. xiv, fig. 13). Some of the adult albinos about three months old were so dark in coloration that they differed very little in general appearance from the usual non-albino types of grey adults of the solitary phase.

The Effect of Crowding on Albinos.

On the 6th of October 1930, 103 newly hatched albino hoppers of the F_2 generation were placed together in a cage 18in. by 9 in. by 15in. (L.p. 544). More than half soon died, and on the 7th of November only 39 were left in the cage, all typical albinos. The behaviour of these hoppers was, broadly speaking, very much like that of an approximately equal number of non-albinos of the same species. There was a considerable amount of jumping, although one got the impression that the albinos did not jump quite so actively as *gregaria* hoppers. Cannibalism and eating of exuviae were observed on several occasions. It can safely be stated that 39 non-albino hoppers, living in a cage of the same size, at the same time, would have produced a large proportion of the *gregaria* type, whether they had been of the solitary or of the swarm type in their first instar. The 39 albinos all remained albinos, showing that the ability to produce the *gregaria* type was not present. In

three of the 39 there was a small amount of brown on the dorsal half of the pronotum, but this was not a dark colour and it could not have been called black; similar darker patches were also present on several of the albinos reared in isolation.

In addition to the crowd in L.p. 544, eight different lots varying from 7 to 52 hoppers of the first instar were crowded together; three of the crowds were of the F_1 generation, three of the F_2 generation, and two of the F_3 generation. The number of hoppers surviving to the fourth and fifth instars varied from 1 to 16, and they were all described as typical albinos.

We may therefore conclude that the albino race of *L. pardalina* will produce albino hoppers whether these are in a dense crowd or isolated. This is confirmed by the fact that the three original albinos were not only recognizable but conspicuous in the large crowd of *gregaria* type hoppers in the cage L.p. 255.

Albinos on growing Grass.

In January 1931 fifteen first instar hoppers of the inbred F_2 generation were placed in celluloid cylinders over growing grass (fig. 202). Four died soon; one lived to the second, 4 to the third, 4 to the fourth and 2 to the fifth instar. Of the eleven, five became green, four remained albinos, and two acquired some green and lost it again (Nos. 692,2 and 692,13) It should be noted that the hoppers described as typical albinos often had a green tinge, and also that several albinos became green in the adult stage in ordinary cages where they were fed two or three times a day only. The fact that five out of eleven albinos acquired a bright green colour is of great interest in connection with the conclusions arrived at elsewhere in this paper, to the effect that green in these insects is in a class by itself. In the case of non-albino hoppers we found that a certain percentage did not become green even under the most favourable conditions. Here again, four out of eleven albinos showed no distinct green, although they were kept under the same conditions as the others.

The albino hoppers that became green had a peculiar type of green colour that can be described as a more or less transparent green; the non-green parts remained a kind of dirty greyish white.

Albinos in Painted Boxes.

One second instar albino of the F_1 generation was placed in a box painted black, in which it lived for 26 days without showing any tendency to develop a darker colour. It died in the black box, in the fifth instar, and was described after death as a typical albino. Another second instar pale green albino was placed in a black box; it died in about a week after losing most of its green colour, but it did not tend to become darker. A third albino, deep green third instar, was transferred to a box painted brown; after moulting to the fourth instar it lost the green and became an ordinary albino, but showed no tendency to resemble the brown box. It died in the fourth instar.

These three tests indicate that the albinos lack the ability to resemble certain colours of the background, which is strongly developed in non-albino hoppers.

Albinos crossed with Non-Albinos.

Albinos were mated with non-albinos of the *gregaria* and *solitaria* types. The types were selected, and the eggs and hoppers were treated in the same way as those of the pairs used in testing the Mendelian segregation hypothesis. Albinos of both sexes were mated with non-albinos of the phases *gregaria* and *solitaria*. About 280 hoppers hatched, but only 65 were reared to the fourth or fifth instars, *i.e.*, about 23%; this was the lowest percentage reared in all our breeding from selected pairs. The 65 hoppers were obtained from the following matings: albino

PLATE XIX.

Figures 53-56: *SCHISTOCERCA GREGARIA* (FORSK.).

Figure

53 ph. *solitaria* ♀ 5th instar, reared in isolation in gauze cylinder painted white, S.g. 43/5, 7 iii. 1931. (× 1·5)

54 ph. *solitaria* ♂ 3rd instar, reared in isolation in gauze cylinder painted white, S.g. 43/6, 14 iii. 1931. (× 1·5)

55 ph. *gregaria* ♀ 5th instar, from cage, 18″×9″×15″, containing about 30 locusts, S.g. 42, 8 ii. 1931. (× 1·5)

56 ph. ? *gregaria* ♀ 4th instar, from cage, 18″×9″×15″; containing about 6 locusts, S.g. 43, 21 iii. 1931. (× 1·5)

Figures 57, 60-62: *LOCUSTA MIGRATORIA MIGRATORIOIDES* (RCH. & FRM.).

57 ph. *solitaria* ♀ 5th instar, from cage, 3′×2½′×2½′, containing about 6 hoppers, S.g. 31, 2 i. 1930. (× 1·5)

60, 61 ph. *gregaria* { 1st instar, from cage, 18″×9″×15″, containing about 100 hoppers, F_5 progeny of field-solitary-phase crowded in cages, L.d. 312, 20 ii. 1931. (× 4)

62 ph. *solitaria* 1st instar, from cage containing a crowd, L.d. 49, 29 x. 1930. (× 4·5)

Figures 58 and 59: *LOCUSTANA PARDALINA* (WALK.).

58 ph. *solitaria* 1st instar, cage-bred, 9 vii. 1930. (× 4)

59 ph. *gregaria* 1st instar, from cage containing a crowd, L.p. 254, January, 1930. (×4)



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male × *gregaria* female, 36; albino male × *solitaria* female, 15; albino female × *gregaria* male, 14.

No albinos appeared in the F_1 generation; the 65 hoppers were mainly of the grey *solitaria* type, but in one lot that were crowded together the swarm type appeared. In other words, the F_1 progeny of albino by non-albino were locusts with the external appearances and behaviour of ordinary forms of the species, showing that the albino type was a recessive. There were some eggs resulting from the inbreeding of the F_1 progeny of these crosses in storage in October 1931. One package was incubated in November 1930, but the eggs failed to hatch.

SCHISTOCERCA GREGARIA (FORSKÅL).

The desert locust, *S. gregaria*, is known in the Union of South Africa only in its phase *solitaria* (=*flaviventris*, Burm.). It is very probable that it occurred in swarms in the past, but the records are rather vague on this point. The species also occurs in South West Africa in the phase *solitaria*, and the phase *gregaria* is supposed to have been recorded from this territory in comparatively recent years.

The writer has taken the phase *solitaria* in the following localities: Kenhardt district north of Brandvlei, Tanqua Valley in southern Calvinia, Vredendal near Klaver, and at Brandvlei. Specimens have also been received from a farm between De Aar and Hope Town. In all these cases the locusts were taken in or near cultivated lands, suggesting that they may have lived as hoppers in the wheat that is grown in these semi-arid regions under irrigation. At Vredendal only one specimen was taken in a field of maize adjoining lucerne lands in which *L. m. migratorioides* were collected; the rest occurred in the stubble of a recently harvested field of wheat about half a mile from the lucerne lands. Only adults have been collected; therefore nothing is known about the immature stages as they occur in the field.

In January 1929 about 30 pairs of adults were collected at Vredendal in the district of Van Rhyns Dorp, and at Brandvlei, Calvinia. In both localities the locusts were found in the stubble of recently cut wheat. They are difficult to catch; we had to stalk up to them very slowly on hands and knees in order to get near enough to strike with the net.

It is worth recording that three species of migratory locusts were taken in the phase *solitaria* within a few yards of one another in the wheat stubble at Nelskop near Brandvlei in January 1929: *L. pardalina*, *L. m. migratorioides* and *S. gregaria*.

Notes on Development.

The 30 pairs of adults of *S. gregaria* were taken to Pretoria and placed in cages. Eggs were laid in February and the resulting hoppers reached the adult stage in May 1929. The F_1 adults lived until about December and a small hatch of F_2 hoppers appeared in November 1929. Adults of the F_2 generation were in the cages from about March to November 1930, and the F_3 hoppers hatched in December 1930.

S. gregaria did not thrive under the conditions which enabled *L. m. migratorioides* to increase to such an extent that we had more material than we needed. Possibly the food may have been unsuitable; Mr. Uvarov tells me that the workers in North Africa find that *S. gregaria* is not primarily a grass feeder in its immature stages.

The P_1 adults brought from the field were placed in egg-tin cages with dry sand in the tins. Some egg packages were laid in dry soil, but we found afterwards that the females prefer to oviposit in moist soil. The females lay more than one egg package in this species; in the cages one laid 5 packages, three laid 4 each, two laid 3 each and four females produced two packages each.

Outdoors in cages the eggs hatched about 14 days after they were laid (April 1929). In an incubator at 31°C. the incubation period varied from 12 to 17 days in observations on 8 packages. Attempts were made to store the eggs at room temperature, in a cool incubator at 12–22°C., and in cold storage near freezing point, for several months, but no hatch could be obtained from eggs treated in these different ways.

The hoppers of the first instar were pale greyish-green in colour. When reared in isolation some remained green (Pl. xix, fig. 53) and others became pale yellowish grey. Great difficulty was experienced in rearing this species in isolation, and only about half a dozen hoppers reached the fifth instar, although we tried to rear them on growing food in celluloid cages, and in various kinds of gauze cages. In some cases the black markings, characteristic of the phase *gregaria*, were faintly indicated on hoppers reared in isolation, but in general isolation produced a more or less uniform coloration of pale green or yellowish grey.

The Phase *gregaria*.

In hoppers reared together in a crowd the black markings, characteristic of the phase *gregaria*, (Uvarov 1928, fig. 88), made their appearance from the third instar onwards. The *gregaria* type produced in the cages differed from that figured in colours by Uvarov (1928, Pl. ix) in being much darker, and in lacking the green colour. Our specimens resembled those figured by Vosseler (1905). On Pl. xix the fourth and fifth instar types of cage-bred *gregaria* are represented (figs. 56 and 55).

In the F_3 generation, a few hoppers hatched in December 1930 which differed from the usual grey-green type in being almost black in the first instar.

The adults obtained from the hoppers reared in crowds were much darker in coloration than those taken in the field, but the pink and yellow colours, characteristic of phase *gregaria* adults in the field, were not observed in the cages. In their structural characters the cage-bred adults showed a distinct tendency to vary in the direction of the phase *gregaria*; the pronotum tended to become smooth and to lose the median keel.

The crowded hoppers were noted as being far less active than those of the three other species of migratory locusts. If the activity of *L. pardalina* is given a "score" of 100%, *S. gregaria* would not reach more than about 25% as observed in our cages. The crowds were not nearly so dense in *S. gregaria* because we could not breed enough hoppers to make dense crowds, and this may partly account for the low "score" for activity. Although their activity was not so spectacular as that of the other species, the *S. gregaria* hoppers developed the *gregaria* coloration when reared under much less crowded conditions, indicating that locustine is produced in this species more readily than in *L. pardalina*.

If the type of coloration figured (figs. 55 and 56) is accepted as being characteristic of the phase *gregaria* as it occurs in swarms in countries invaded by this species, we may conclude that the cage experiments in crowding the *solitaria* hoppers resulted in the transformation of *solitaria* into *gregaria*.

OBSERVATIONS ON NON-MIGRATORY GRASSHOPPERS.

The Effect of Crowding.

Oedaleus nigrofasciatus (De Geer).

During April and May 1929 about 20 female and 20 male adults of this species were collected in Pretoria and put in a cage (18in. by 9in. by 15in.) on an egg drawer. In July eight egg packages were found in the drawer. The cage was left out in the sun and the soil was watered during October. In November about 400 nymphs hatched; they were grey in the first instar, with brown markings.

On 5th December about 300 nymphs were crowded together in one half of an incubator cage (fig. 197); they were kept outdoors, and fed on green grass. The striking difference between these nymphs and those of *Locustana* and *Locusta* in adjoining cages was the lack of activity in *Oedaleus*. Living under identical conditions of temperature, humidity and light, the *Oedaleus* nymphs showed no tendency to develop the swarm activity that was such a conspicuous feature in the cages containing hoppers of *Locustana* and *Locusta*. It should be noted that the *Oedaleus* nymphs were living under very crowded conditions, about 300 being confined in a very small space.

On 15th January, 41 days after they were put into the small cage, the insects were taken out and described. There were 2 adults and 40 nymphs: 12 in the fifth instar, 26 in the fourth and 2 in the third. The colours varied from pinkish grey and light grey to green, yellow and dark grey-brown; about 20 of the 40 nymphs were classed as dark grey-brown.

On 6th December 1929, nine nymphs (first and second instar) were isolated in galvanized gauze cylinders. On 15th January 7 of these were alive in the fifth instar: they were described as follows: 2 dark grey-brown, 2 pink, 2 light grey and yellow, 1 green. The two dark nymphs were practically as dark as the darkest nymphs reared in the crowd.

These experiments show: (1) that crowding does not produce colours in the nymphs of *O. nigrofasciatus* which do not also appear in those reared in isolation; and (2) that the nymphs of this species do not stimulate one another into jumping activity when they are crowded together.

Acanthacris ruficornis (F.).

From April to June 1929 about 40 adults of this common large garden grasshopper were collected in Pretoria and placed together in cages on egg drawers. The pale green nymphs of the first instar appeared in December 1929 in the cages which had been kept outdoors. The surviving nymphs became adults about March 1930, indicating that there is only one generation of this species per annum.

Several hundreds of nymphs hatched in the two cages during the summer of 1929–30, but only about 80 hoppers survived. Some of the nymphs were crowded together in a small cage 6in. by 4½in. by 6in., and others were kept in larger cages. About 30 were isolated in galvanized gauze cylinders, and 10 of these lived to the fifth instar. They were fed on grass, maize and the leaves of the Jerusalem artichoke.

In general, the results were very similar to those obtained with *Oedaleus*. There were many different colour types both in the isolated and crowded nymphs, from pale yellow, pink and green, to light grey and grey-brown. Some of the isolated nymphs were almost as dark in colour as the darkest individuals in the cages containing crowds.

As in the case of *Oedaleus*, the nymphs of *Acanthacris* did not stimulate one another into the kind of activity that develops in crowds of *Locustana* and *Locusta*.

Resemblance to the Colour of the Environment.

Sphingonotus scabriusculus, Stål, has been mentioned in preceding sections as the grasshopper most commonly associated with the phase *solitaria* of *L. pardalina* in its permanent habitat.

In February 1931 the writer collected some nymphs of *S. scabriusculus* at Hope Town on the calcrete-pebble veld; the majority were dirty greyish-white with minute black specks resembling the calcrete very closely.

Five dirty-white nymphs were placed on black backgrounds in their third instar: in a painted box one was noted in the fifth instar as showing no resemblance to

black ; in painted gauze cylinders one had slight resemblance in the fourth, one had fair resemblance in the fifth, and two were noted as " good imitation of black " in the fifth instar after 33 and 38 days respectively.

One bluish-black nymph (from the veld) was placed in a box painted white in its fourth instar ; after 23 days it was noted in the fifth as " dark greyish-blue, slight imitation." One fourth instar nymph (dirty-white) was kept in a green box for 21 days ; in the fifth it had no trace of green. Another nymph lived from the third to the fifth instar in celluloid over growing grass for 28 days ; it remained dirty-white.

These tests indicate that the nymphs of *S. scabriusculus* tend to imitate the colour of the background on which they are reared. The imitation of the background was not so striking as in *L. pardalina* and *L. migratorioides*, and it did not develop so rapidly ; this may be due to a slower rate of growth in the nymphs of *S. scabriusculus*.

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Explanation of Plate XX.

Locustana pardalina (Walker).

Extreme solitary phase (left), and extreme swarm phase (right), both taken in the field.

Figs. 63–65. ph. *solitaria* ♂♂ from the field, De Aar, C.P., February 1931.

,, 66–67. ph. *solitaria* ♀♀ from the field, De Aar, C.P., February 1931.

,, 68–69. ph. *gregaria* ♂♂ from large migrating swarms, Graaff Reinet, C.P., 1921–1922.

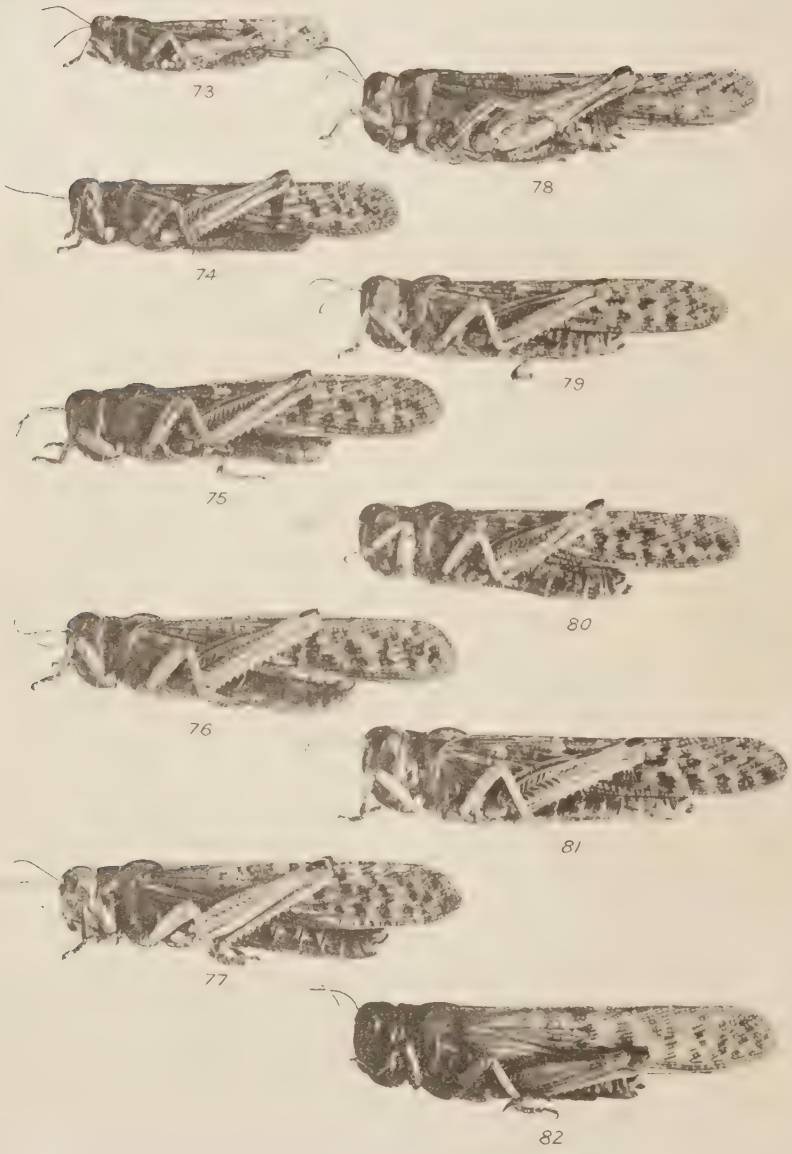
Fig. 70. ph. *gregaria* ♂ from large migrating swarm Potgietersrust, Transvaal, 16.iv.1906.

Figs. 71–72. ph. *gregaria* ♀♀ from large migrating swarms, Graaff Reinet, C.P., 1921–1922.

All figures natural size.



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Explanation of Plate XXI.

Locustana pardalina (Walker).

F_4 cage-bred, crowded progeny of solitary phase from the field (figs. 74–76 and 79–81) compared with extreme field *solitaria* (73 and 78) and extreme field *gregaria* (77 and 82).

Figs. 73 and 78.	ph. *solitaria*	♂♀ from the field, Graaff Reinet, C.P., 24.iii.1920.
,, 74–76 and 79–81.	ph. *gregaria*	♂♂ and ♀♀ cage-bred, L.p. 629, F_4 progeny of field solitary phase, crowded in cages, 15.xii.1930. 74 and 79 smallest ♂♀ of pinned series. 75 and 80 intermediate-sized ♂♀. 76 and 81 largest ♂♀ of pinned series.
,, 77 and 82.	ph. *gregaria*	♂♀ from large migrating swarms, Graaff Reinet, C.P., 1921–1922.

All figures natural size.

Explanation of Plate XXII.

Locustana pardalina (Walker).

Males.—F_2, F_3 and F_4 progeny of *solitaria* from the field, crowded in cages (figs. 84–86 and 89-91) compared with extreme field *solitaria* (83 and 88) and extreme field *gregaria* (87 and 92).

Fig. 83. ph. *solitaria* ♂ from the field, Fauresmith, O.F.S., 2.iii.1929. Smallest specimen available.

,, 88. ph. *solitaria* ♂ from the field, Fauresmith, O.F.S., 21.ii.1928. Largest specimen available.

Figs. 84 and 89. ph. ? *transiens* ♂♂ cage-bred F_2, L.p. 233, May–June 1929. 84 : smallest ; 89 : largest pinned specimen.

,, 85 and 90. ph. *gregaria* ♂♂ cage-bred F_3, L.p. 255, December 1929. 85 : smallest ; 90 : largest pinned specimen.

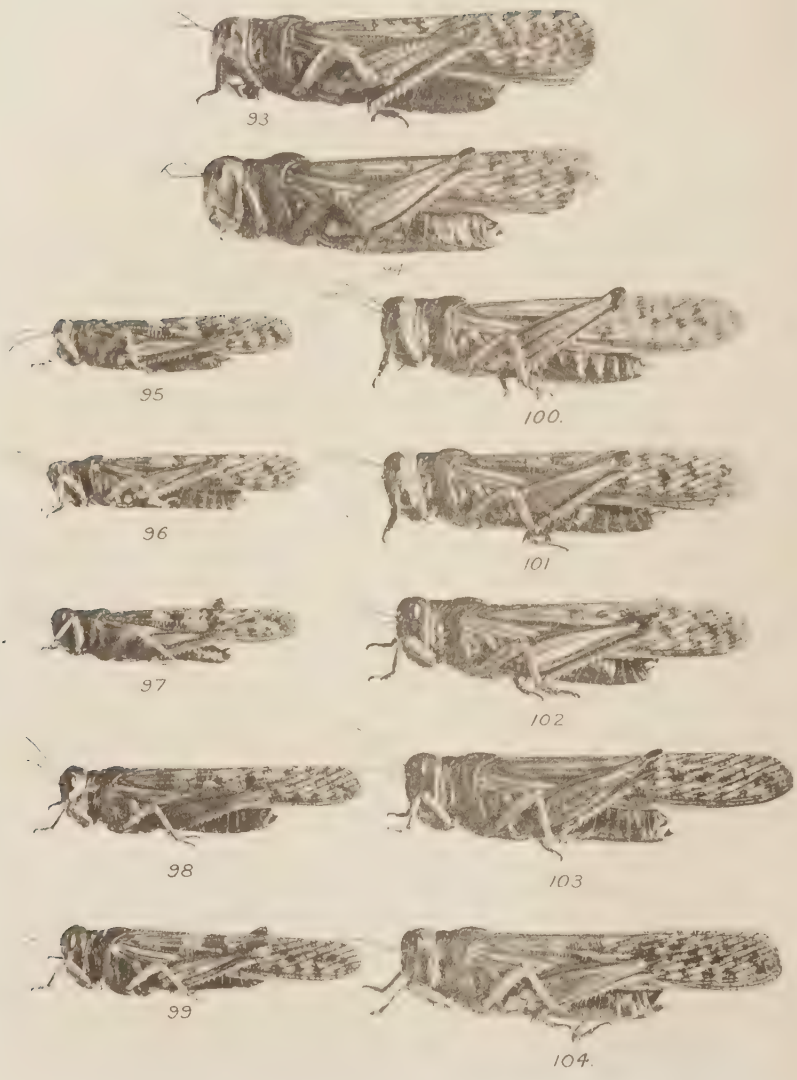
,, 86 and 91. ph. *gregaria* ♂♂ cage-bred F_4, L.p. 629, 15.xii.1930. 86 : smallest ; 91 : largest pinned specimen.

,, 87 and 92. ph. *gregaria* ♂♂ from large migrating swarms, Graaff Reinet, C.P., 1921–1922. 87 : smallest ; 92 : largest pinned specimen.

All figures natural size.



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Explanation of Plate XXIII.

Locustana pardalina (Walker).

The effect of crowding and isolation on the F_1 progeny of a pair of swarm type locusts.

Fig. 93. ♂ parent, was perfect *gregaria* type hopper in fifth instar. L.p. 352, 18.iii.1930.

,, 94. ♀ parent, was perfect *gregaria* type hopper in fifth instar. L.p. 352, 18.iii.1930.

Figs. 95–97. Three ♂♂ } F_1 progeny of the pair L.p. 352 (figs. 93–94), reared
,, 98–99. Two ♀♀ } in isolation, each in its own cage.
L.p. 352/51, /33, /31, /53, and /44. 25.xi.1930.

,, 100–102. Three ♂♂ } F_1 progeny of the pair L.p. 352 (figs. 93–94) from a
,, 103–104. Two ♀♀ } cage 6in. by 4½in. by 6in. containing 10 locusts.
L.p. 352B. 15.xii.1930.

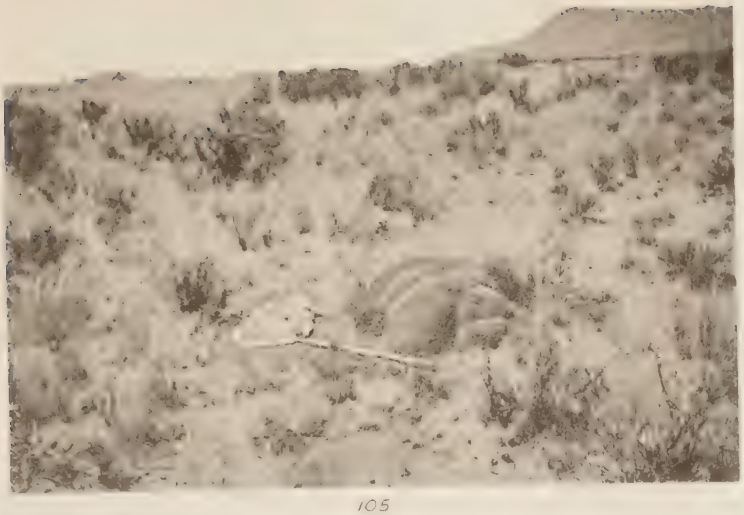
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Explanation of Plate XXIV.

Types of veld vegetation in the permanent breeding grounds of *Locustana pardalina* (Walker).

Fig. 105. Reddish " Kalahari blown " sand in district of Hope Town, C.P. Grasses largely *Aristida barbicollis*, Trin & Rupr., and *Eragrotis lehmanniana*, Nees.
Nest of *Trinervitermes* in foreground. The ph. *solitaria* is rarely found in this type of habitat, but incipient and large swarms tend to select it for oviposition.

,, 106. Lime-stone area, Hope Town, C.P. Short scrub bushes mainly *Pentzia* ; very short tufts of grass : *Eragrostis truncata*, Hack., *Enneapogon brachystachys*, Stapf, *Tragus racemosus*, All., and *Eragrostis major*, Host.
Pocket watch in foreground to show height of bushes. White pebbles are calcrete. This type of habitat is favoured by the hoppers and adults of the ph. *solitaria*.



105



106.

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101



108

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Explanation of Plate XXV.

Types of veld vegetation in the permanent breeding grounds of *Locustana pardalina* (Walker).

Fig. 107. Hard, stony soil with shale on surface, De Aar, C.P. Grass taller and denser than on lime-stone (fig. 106); scattered Karroo-bush (*Pentzia* et al.).
This type of veld is also a habitat of the ph. *solitaria*.

,, 108. Red sand with rather close growth of "driedoring" (*Rhigozum trichotomum*, Burch.) Hope Town, C.P.
The ph. *solitaria* does not usually occur in this type of habitat.

Explanation of Plate XXVI.

Males of four species of African migratory locusts, all of the phase *gregaria*.

Fig. 109. *Locustana pardalina* (Walker), Graaff Reinet, C.P., 1921–1922.

,, 110. *Locusta migratoria migratorioides*, Rch. & Frm., Wad Medani, Sudan, 1930.

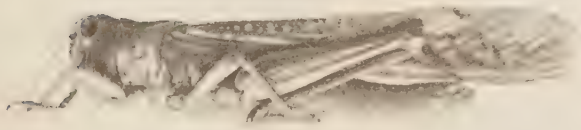
,, 111. *Schistocerca gregaria* (Forsk.), Tanganyika, April 1929.

,, 112. *Nomadacris septemfasciata* (Serv.), Ngamiland, Northern Bechuanaland, April 1931.

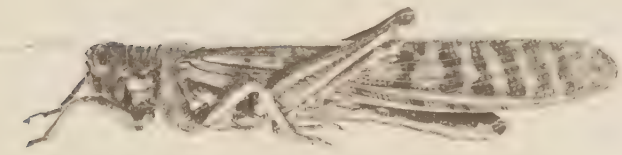
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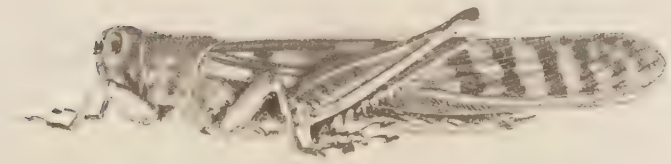
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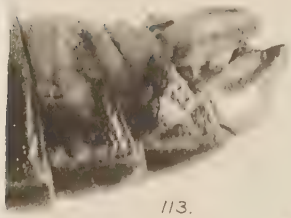


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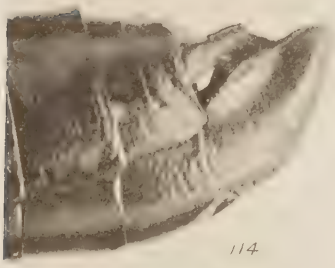
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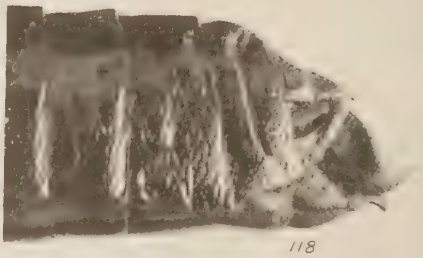
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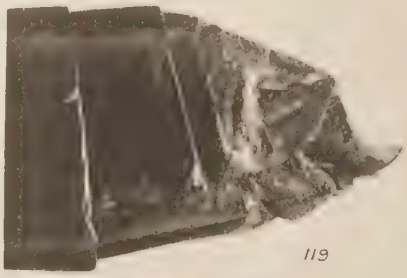
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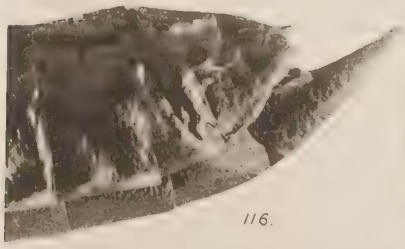
118



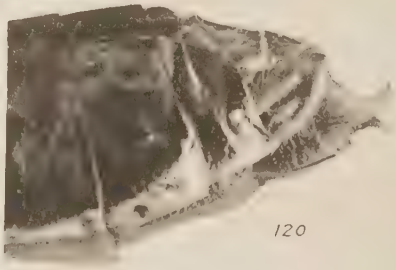
115



119



116.



120

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Explanation of Plate XXVII.

Four species of African migratory locusts.

Posterior extremity of abdomen of both sexes, all of phase *gregaria*.

Figs. 113 and 117. ♂ and ♀ *Locustana pardalina* (Walker).

,, 114 and 118. ♂ and ♀ *Locusta migratoria migratorioides*, Rch. & Frm.

,, 115 and 119. ♂ and ♀ *Schistocerca gregaria* (Forsk.).

,, 116 and 120. ♂ and ♀ *Nomadacris septemfasciata* (Serv.).

All figures enlarged (× 6).

Explanation of Plate XXVIII.

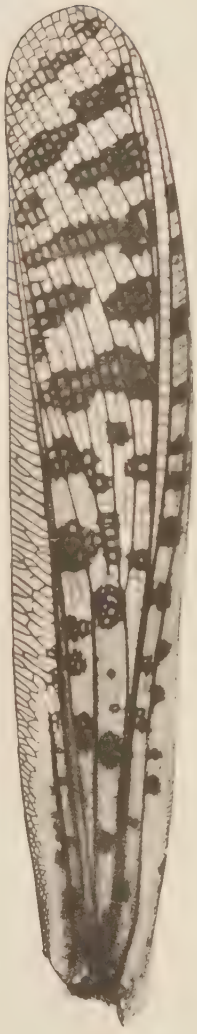
Fig. 121. Left fore-wing of *Nomadacris septemfasciata* (Serv.) phase *gregaria*. Note fine reticulation in basal third.

,, 122. Left fore-wing of *Schistocerca gregaria* (Forsk.) phase *gregaria*.

Both figures enlarged (× 2·2).



121.



122.

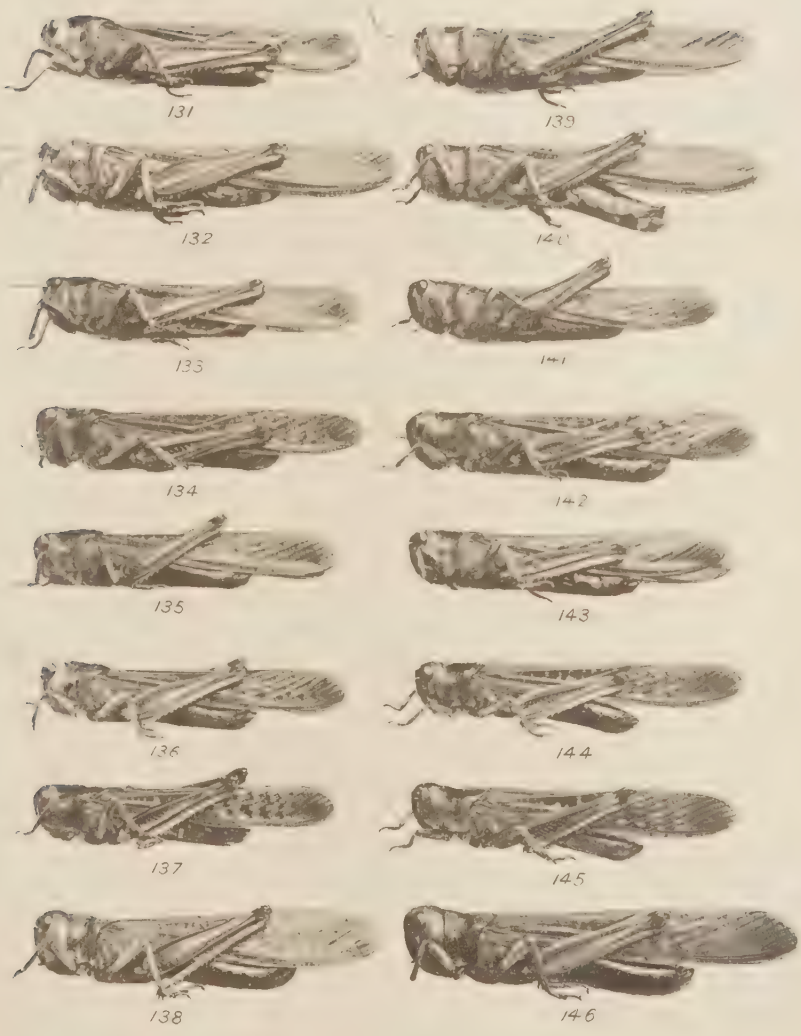
Explanation of Plate XXX.

Locusta migratoria migratorioides, Rch. & Frm.

Males.—Cage-bred specimens (figs. 133–137 and 141–145), the crowded progeny of ph. *solitaria* from the field, compared with ph. *solitaria* (figs. 131 and 139) and ph. *gregaria* (figs. 132, 138, 140 and 146).

Figs.	131–138.		Left-hand column, are specimens selected from the pinned series available as showing the highest arched or least concave pronotum represented in their respective groups.
,,	139–146.		Right-hand column, are specimens selected from the pinned series available as showing the lowest arched or most concave pronotum represented in their respective groups.
,,	131 and 139.	ph. *solitaria*	From the field, Vredendal, Van Rhyns Dorp, C.P., Dec. 1930 to Jan. 1931. L.d. 568.
,,	132 and 140.	ph. *gregaria*	From migrating swarms, Makoni, Southern Rhodesia. 17.ix.1923.
,,	133 and 141.	ph. ? *transiens*	F_1 Cage-bred, L.d. 41, 30.v.1929.
,,	134 and 142.	ph. ? *gregaria*	F_2 Cage-bred, L.d. 45 and 49, Jan. 1930.
,,	135 and 143.	ph. *gregaria*	F_3 Cage-bred, L.d. 41 and 49, May 1930.
,,	136 and 144.	ph. *gregaria*	F_4 Cage-bred, L.d. 45, Dec. 1930.
,,	137 and 145.	ph. *gregaria*	F_5 Cage-bred, L.d. 49, 21.v.1931.
,,	138 and 146.	ph. *gregaria*	From migrating swarms, Shinyanga, Tanganyika, March 1931.

All figures reduced (× 0·84).



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Explanation of Plate XXXII.

Locusta migratoria migratorioides, Rch. & Frm.

The effect of crowding and isolation on the F_1 progeny of a pair of solitary type locusts.

Fig. 163–164. Two ♂♂ } F_1 progeny of the pair L.d. 223 reared in isolation, each
,, 165–166. Two ♀♀ } in its own cage.
L.d. 223 2, 5, 14, 15, Feb.–March 1931.

,, 167–168. Two ♂♂ } F_1 progeny of the pair L.d. 223, from a cage 18in. by
,, 169–170. Two ♀♀ } 9in. by 15in. containing about 60 locusts, March–April
1931.

All figures natural size.



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Explanation of Plate XXXIV.

Schistocerca gregaria (Forsk.).

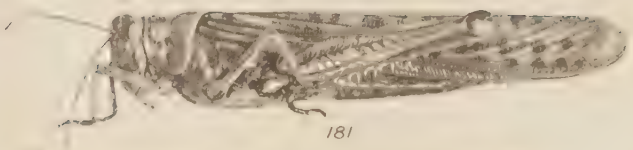
Fig. 181. ph. *solitaria* ♀ from the field, Vredendal, Van Rhyns Dorp, C.P., January 1929.

,, 182. ph. *transiens* ♂ F_3, bred in cages (more or less crowded). S.g. 53, 15.iv.1931.

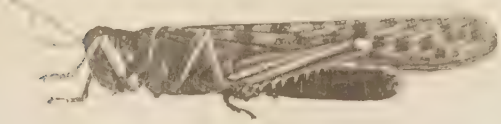
Figs. 183 and 184. ph. *transiens* ♀♀ F_3, bred in cages (more or less crowded). S.g. 53, 15.iv.1931.

,, 185 and 186. ph. *gregaria* ♂♀ from migrating swarms, Tanganyika, April 1929.

All figures natural size



181



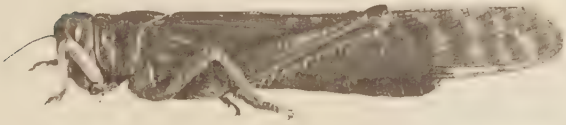
182.



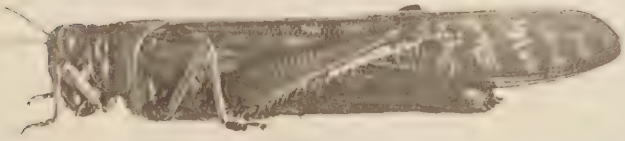
183



184.



185



186.

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Explanation of Plate XXXVI.

Fig. 189. Double breeding cage of wood and galvanized wire gauze, each half 18in. by 9in. by 15in. inside measurements above surface of soil in drawer. Glass front, sliding glass door. Slide of galvanized iron runs above drawer.

,, 190. Double cage like fig. 189, except that drawers are suspended on metal strips running in grooves.

,, 191. Double cage of wood and galvanized wire gauze, each half 18in. by 9in. by 15in. Floor of wood with hole for egg tin and metal slide to cover hole when tin is removed.

,, 192. Table for three cages, with rain-cover.

,, 193. *Locusta migratoria migratorioides*, Rch. & Frm., hoppers about 15 minutes after emerging above ground. Note white skins of the "intermediate" moult.

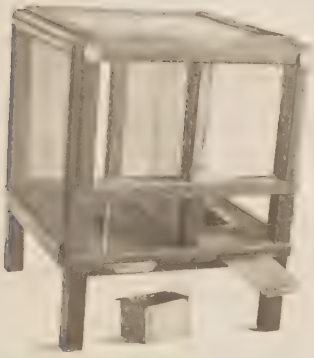
,, 194. Table with canopy of calico used for "painted-box" cages.



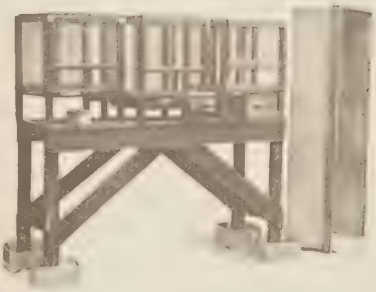
189



190



191



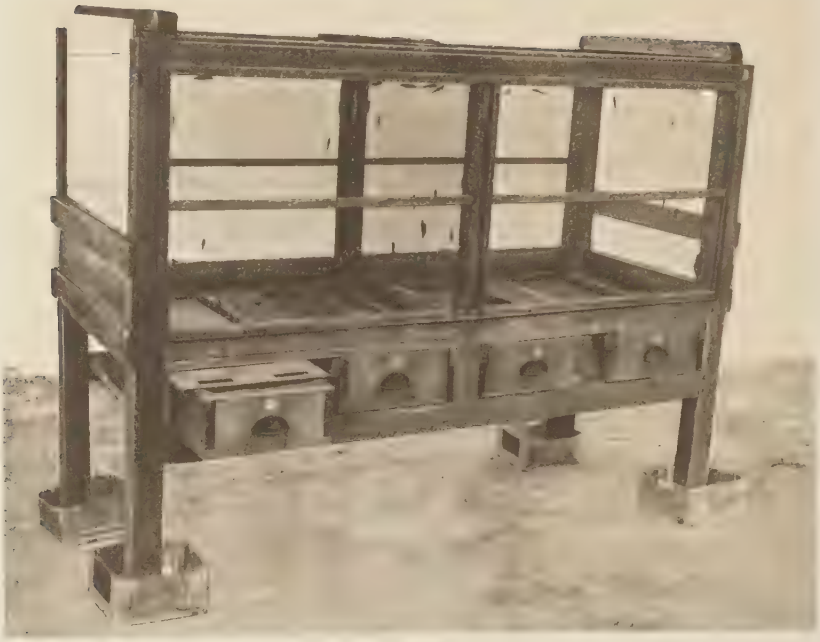
192



193



194



195



196.

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Explanation of Plate XXXVII.

Large breeding cage, inside measurements (excluding drawers) 6ft. by 2½ft. by 2½ft. Divided into two equal halves by means of a gauze partition. Upper sliding glass door of plate glass moves vertically; lower sliding glass door moves horizontally. One metal slide in place over a drawer.

Fig. 195. Cage uncovered.

,, 196. Rain-proof cover of galvanized iron in place over the cage.

Explanation of Plate XXXVIII.

Fig. 197. Incubator cage, inside measurements 12in. by 6in. by 4½in. Metal or glass slide divides cage into two equal halves. Sliding glass doors, moving vertically in grooves. Left half with egg-tin in place and metal slide over egg-tin.

,, 198. Set of four cages used in "painted box" experiments. Each cage 9in. by 5½in. by 3½in. inside measurements. Note air holes about ½in. in diameter and sliding glass lids in two unequal parts.

,, 199. Apparatus used in "forced activity" experiments. Table 5ft. long, same as table in fig. 192. Note revolving arms of strap-iron adjusted to strike the sets of celluloid cages.

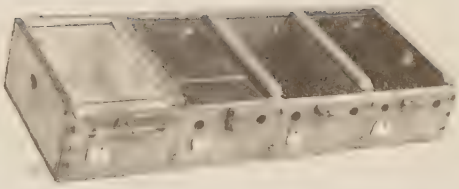
,, 200. "Gauze cylinder" cages, each cage about 4½in. by 4½in., used for rearing hoppers in isolation.

,, 201. Set of eight celluloid cages used in "forced activity" experiments (fig. 199)), each cage about 4½in. by 2½in. at the base, 4in. by 1¾in. at the top and about 4in. in height. Note sliding doors of perforated zinc. Cages are glued to a sheet of heavy celluloid.

,, 202. Celluloid cylinders over growing barley, each cylinder about 3in. by 8in.



197



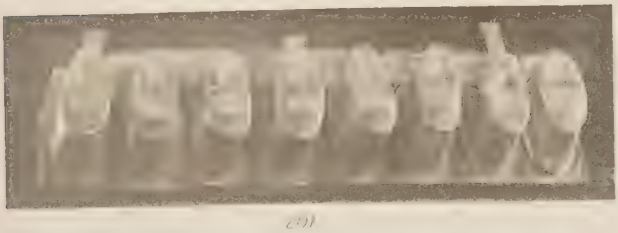
198



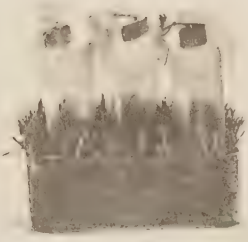
199



200.



201



202

COLLECTIONS RECEIVED.

The following collections were received by the Imperial Institute of Entomology between 1st April and 30th June, 1932, and the thanks of the Managing Committee are tendered to the contributors for their kind assistance :—

Mr. A. M. Altson : —2 *Stomoxys*, 157 other Diptera, 2 Lepidoptera, and 5,000 Mites ; from Northern Rhodesia.

Mr. D. J. Atkinson : —36 Parasitic Hymenoptera ; from Burma.

Mr. M. D. Austin :—143 Parasitic Hymenoptera ; from England.

Mr. G. Babault : —87 Coleoptera and 39 Orthoptera ; from the Belgian Congo.

Mr. E. Ballard, Government Entomologist : —120 Lepidoptera, 2 Rhynchota, 4 Planipennia, and 29 Odonata ; from Palestine.

Dr. H. F. Barnes :—12 Parasitic Hymenoptera ; from England.

Mr. B. Blumberg : —20 Dipterous early stages, 10 Coleopterous larvae, 5 Thysanoptera, 27 Rhynchota, 3 Collembola, 18 Spiders, 13 Centipedes, 3 Millipedes, 20 Oligochaeta, and 42 Crustacea ; from Queensland, Australia.

Dr. G. Bondar :—4 Curculionidae ; from Brazil.

Prof. W. H. Brittain :—504 Coleoptera ; from Canada.

Mr. H. Britten : —57 Parasitic Hymenoptera and 29 cocoons ; from England.

Mr. G. Bunzli : —500 Formicidae, 23 species of Coccidae, 2 species of Aphidae, and 51 other Rhynchota ; from Dutch Guiana.

Dr. P. A. Buxton, London School of Tropical Medicine :—15 Coleoptera, 2 Planipennia and 2 cocoons ; from various localities.

Mr. J. Carroll :—1 species of Coccidae ; from Ireland.

Dr. A. Chiaromonte :—1 Moth ; from Italian Somaliland.

Chief Entomologist, Pretoria : —68 Coleoptera, 10 Parasitic Hymenoptera, 4 other Hymenoptera, 9 Lepidoptera, 28 Rhynchota, 3 Orthoptera, and 50 Parasitic Worms ; from South Africa.

Mr. A. F. Clark :—7 Coleoptera ; from New Zealand.

Colombian Consul, London :—4 Orthoptera ; from Colombia.

Mr. G. H. Corbett, Government Entomologist : —89 Diptera and 14 pupa cases, 46 Coleoptera, 296 Parasitic Hymenoptera, 12 other Hymenoptera, 109 Lepidoptera and 10 cocoons, 32 Isoptera, 30 Thysanoptera, 3 species of Coccidae, 1 species of Aphidae, 32 other Rhynchota, 8 Psocidae, 4 Orthoptera, 20 Collembola, and 1,000 Mites ; from Malaya.

Mr. G. S. Cotterell, Government Entomologist : —4 Diptera, 39 Coleoptera, 21 Parasitic Hymenoptera, 2 other Hymenoptera, 89 Lepidoptera, and 30 Rhynchota ; from the Gold Coast.

Mr. A. Cuthbertson, Assistant Entomologist :—79 Diptera, and 37 Rhynchota ; from Southern Rhodesia.

Dr. J. Deshusses :—17 Parasitic Hymenoptera ; from Switzerland.

Director of Agriculture, Gambia :—1 species of Aphidae ; from the Gambia.

Director of Agriculture, Seychelles :—2 species of Coccidae ; from the Seychelles.

Dominion Entomologist, Ottawa :—4 Parasitic Hymenoptera and 13 Tenthredinidae ; from Canada.

Dr. H. Eltringham :—12 Dipterous larvae ; from England.

Entomologist, Bangalore :—6 Tabanidae, 39 other Diptera, 21 Coleoptera, 5 Parasitic Hymenoptera, 5 other Hymenoptera, and 8 Orthoptera ; from Mysore, India.

Mr. Escherich :—3 Parasitic Hymenoptera ; from Germany.

Mr. J. L. Froggatt :—30 Parasitic Hymenoptera ; from New Guinea.

Mr. S. Garthside :—25 Parasitic Hymenoptera and 3 cocoons, 3 Lepidoptera, and 6 Hemerobiidae ; from England.

Mr. F. D. Golding, Government Entomologist :—2 Diptera, 10 Coleoptera, 75 Parasitic Hymenoptera, 50 other Hymenoptera, 33 Lepidoptera, 2 species of Aleurodidae, 2 other Rhynchota, and 80 Orthoptera ; from Nigeria.

Government Entomologist, Lyallpur :—150 Parasitic Hymenoptera ; from the Punjab, India.

Mr. W. Greenwood :—92 Lepidoptera ; from the Fiji Islands.

Dr. W. J. Hall :—5 Parasitic Hymenoptera ; from Southern Rhodesia.

Mr. G. L. R. Hancock, Assistant Entomologist :—14 Tabanidae, 190 other Diptera, 196 Coleoptera, 32 Parasitic Hymenoptera, 9 other Hymenoptera, 32 Lepidoptera, 2 slides of Thysanoptera, 6 species of Coccidae, 18 species of Aphidae, 2 species of Aleurodidae, 30 Cimicidae, 153 other Rhynchota, 15 Orthoptera, and 4 slides of Mites ; from Uganda.

Mr. E. Hargreaves, Government Entomologist :—8 Coleoptera, 10 Parasitic Hymenoptera, 150 other Hymenoptera, 81 Lepidoptera, and 3 larvae, 20 Thysanoptera, 3 species of Coccidae, 1 species of Aphidae, 9 Orthoptera, and 50 Mites ; from Sierra Leone.

Mr. W. V. Harris :—83 Coleoptera, 4 Parasitic Hymenoptera, 19 other Hymenoptera, 3 Lepidoptera, 15 Thysanoptera, 2 species of Coccidae, 3 species of Aleurodidae, 57 other Rhynchota, 73 Orthoptera, 4 Dermaptera, 3 Chrysopidae, and 12 Chelifers ; from Tanganyika Territory.

Mr. G. V. Hudson :—158 Coleoptera ; from New Zealand.

Dr. A. D. Imms :—9 Parasitic Hymenoptera ; from England.

Independent Biological Laboratories, Tel-Aviv :—3 Formicidae and 2 Collembola ; from Palestine.

Indian Lac Research Institute, Namkum :—22 Parasitic Hymenoptera ; from India.

Inspector-General of Agriculture, Baghdad :—1 Coleopterous larva ; from Iraq.

Mr. S. G. Jary :—5 Tenthredinidae ; from England.

Mr. C. King :—14 Culicidae, 20 other Diptera, 67 Coleoptera, 8 Hymenoptera, 352 Lepidoptera, 2 Isoptera, 19 Rhynchota, 6 Orthoptera, and 26 Odonata ; from Southern Nigeria.

Mr. C. B. R. King :—20 Parasitic Hymenoptera and 2 cocoons, and 3 Lepidoptera ; from Ceylon.

Mr. W. R. S. Ladell :—5 Tabanidae, 28 other Diptera, 296 Coleoptera, 6 Hymenoptera, 810 Lepidoptera, 458 Rhynchota, and 7 Orthoptera ; from Siam.

Dr. W. A. Lamborn, Medical Entomologist :—100 *Tabanus* larvae, 47 *Stomoxys*, 22 *Lyperosia*, 6 Cecidomyiid galls, 230 other Diptera and 30 pupa cases, 9 Curculionidae and 20 pupa cases, 800 Parasitic Hymenoptera and 20 cocoons, 4 other Hymenoptera, 7 Lepidoptera and 4 pupa cases, 2 Rhynchota and 8 nymphs, 33 Planipennia and 22 cocoons, and 10 Mites on 2 Muscidae ; from Nyasaland.

Dr. S. Leefmans :—32 Coleoptera, 35 Lepidoptera, and 22 Rhynchota ; from the Dutch East Indies.

Mr. D. de Leon :—60 Parasitic Hymenoptera ; from Germany.

Mr. R. A. Lever, Government Entomologist :—14 Siphonaptera, 8 Nycteribiidae, 26 Culicidae, 5 Tabanidae, 6 Hippoboscidae, 3 *Lyperosia*, 93 other Diptera, 450 Coleoptera, 28 Parasitic Hymenoptera, 107 other Hymenoptera, 64 Lepidoptera, 20 Isoptera, 5 species of Coccidae, 142 other Rhynchota, 15 Orthoptera, 2 Planipennia larvae, 10 Mallophaga, 2 Ticks, 2 species of Fungus, 22 Shells, and 5 Birds ; from the Solomon Islands.

Mr. A. Da Costa Lima :—3 Parasitic Hymenoptera ; from Brazil.

Dr. D. Miller, Cawthron Institute :—2 Curculionidae and 27 Parasitic Hymenoptera ; from New Zealand.

Mr. H. M. Morris, Government Entomologist :—110 Lepidoptera ; from Cyprus.

Mr. M. C. Mossop :—4 Coleoptera, 8 Parasitic Hymenoptera, 2 Lepidoptera, and 1 species of Aleurodidae ; from Southern Rhodesia.

Mr. J. Muggeridge, Entomologist :—4 Coleoptera and 10 Mites ; from New Zealand.

Natal Museum, Pietermaritzburg :—6 *Stomoxys* ; from South Africa.

Mr. R. W. Paine :—176 Culicidae, 2 other Diptera, 5 Coleoptera and 3 larval skins, 67 Parasitic Hymenoptera, 5 other Hymenoptera, 10 Thysanoptera, 11 Dermaptera, and 9 Crustacea ; from Java and Fiji.

Prof. W. S. Patton :—10 Parasitic Hymenoptera and 38 Isoptera ; from England and Sierra Leone.

Mr. H. M. Pendlebury, F. M. S. Museum :- 262 Coleoptera ; from Malaya.

Mr. W. H. Potts :—86 Orthoptera ; from Tanganyika Territory.

Prof. E. B. Poulton :—23 Coleoptera ; from Africa.

Mrs. M. C. Rant :—2 Rhynchota, 63 Orthoptera, and 4 Planipennia ; from Arabia.

Mr. Y. R. Rao, Locust Investigator :-6 Coleoptera, 3 Lepidoptera, and 17 Orthoptera ; from Baluchistan.

Dr. A. Reyne :—1 Acridid ; from Celebes.

Mr. E. Riggert :—5 Parasitic Hymenoptera ; from Germany.

Mr. J. I. Roberts, Medical Entomologist :—33 Rodents ; from Kenya Colony.

Mr. Nihat Schewket Bey :—9 Diptera, 184 Coleoptera, 14 Parasitic Hymenoptera, 37 Rhynchota, 27 Orthoptera, and 500 Snail Shells ; from Asiatic Turkey.

Mr. H. W. Simmonds, Government Entomologist :—9 Diptera, 5 Parasitic Hymenoptera, and 2 Rhynchota ; from the Fiji Islands.

Mr. C. Smee, Government Entomologist :—300 Isoptera ; from Nyasaland.

Mr. H. D. Smith :—4 Parasitic Hymenoptera ; from France.

Mr. E. R. Speyer :- 140 Diptera and 25 early stages, 2 species of Aphidae, 40 Collembola, 100 Mites, 14 Symphylidae, and 7 Annelidae ; from the British Isles.

Mr. F. A. Squire :—13 Culicidae, 19 other Diptera, 18 Coleoptera, 15 Parasitic Hymenoptera, 31 other Hymenoptera, 5 Lepidoptera, 21 Rhynchota, 6 Orthoptera, and 4 Odonata ; from British Guiana.

Systematic Entomologist, Dehra Dun :—16 Coleoptera, 44 Parasitic Hymenoptera, and 47 Psyllidae ; from the United Provinces, India.

Mr. O. H. Swezey :—6 Coleoptera and 9 Parasitic Hymenoptera ; from Honolulu.

Mr. A. W. Taylor :—105 Culicidae ; from Northern Nigeria.

Mr. J. S. Taylor :—900 Coleoptera and 561 Rhynchota ; from South Africa.

United States National Museum, Washington :—4 Parasitic Hymenoptera ; from the United States of America.

Mr. R. Veitch, Chief Entomologist :—338 Diptera and 51 puparia ; from Queensland, Australia.

Mr. F. Weber :—115 Culicidae ; from Brazil.

Wellcome Tropical Research Laboratories, Khartoum :—3 Nycteribiidae, 11 Culicidae, 123 other Diptera, 55 Coleoptera, 150 Parasitic Hymenoptera, 40 other Hymenoptera, 58 Lepidoptera, and 8 species of Aphidae ; from the Sudan.

Dr. F. Zacher :—4 Coleoptera and 7 Parasitic Hymenoptera ; from Germany and Tanganyika Territory.

THE LARGE NARCISSUS FLY, *MERODON EQUESTRIS*, FAB. (SYRPHIDAE).

By W. E. H. Hodson, A.R.C.S., D.I.C.

The University, Reading.

(Plate XXXIX.)

Introduction.

Larvae of the Syrphid fly, *Merodon equestris*, known throughout Europe and North America as the Large Narcissus Fly or Large Bulb Fly, attack and destroy narcissi and various other bulbous-rooted plants. A considerable volume of literature has accumulated, more particularly during the past eighteen years, concerning the life-history and control of the pest. A perusal of this literature discloses the existence of numerous discrepancies of opinion amongst authorities on certain fundamental points. For example, some writers maintain that larvae can take two seasons to reach maturity, others definitely state that one year only is required. Again, considerable uncertainty has existed as to the manner in which larvae enter bulbs and dates at which oviposition and pupation are to be expected. Further, more serious from the economic point of view, in spite of the accumulation of literature it can be stated quite definitely that the fly has continued annually to increase in numbers. At the present time commercial growers in Britain are faced with yearly losses of many thousands of pounds worth of valuable bulbs as a direct outcome of fly infestations and it has become increasingly clear that concerted action amongst growers is essential in order that such losses may be diminished.

The writer has been associated for a number of years with the commercial bulb industry and the present publication is the outcome of work and observation extending over eight seasons. The work has been assisted during its latter stages by a Special Research Grant provided by the Ministry of Agriculture and Fisheries.

It is proposed to review in detail the life-history of the fly and to bring forward further evidence concerning the possibilities of obtaining control of the pest under field conditions.

Historical.

The genus *Merodon* is essentially a Southern European one, although a limited number of species occur elsewhere, and the species *M. equestris* is rapidly becoming cosmopolitan. The fly was first recorded in England on 8th June 1869, when Verrall[23] captured a specimen in a south London garden. Verrall noted that the garden had for many years been planted with narcissus bulbs imported from Holland and concluded that the species was imported about that time. By 1896 the fly had become so common that articles commenced to appear concerning the ravages occasioned to narcissus plantations in Cornwall and elsewhere.

Writing in 1914, Fryer[6] stated that the fly occurs in England, Scotland, Wales, and Ireland, and is supposed to have been imported, probably from Holland, but that Theobald considered it native. Theobald based this suggestion on the fact that he had taken the larva in the wild hyacinth, *Scilla nutans*. In the same paper Fryer suggested destroying the larvae by steeping infested bulbs in warm water for from 24 to 48 hours. One year later Fryer[8] improved upon this suggestion and showed that steeping dormant bulbs in water heated to 110°F. for one hour effected a hundred per cent. kill of the larvae, without apparent injury to the bulbs. Fryer carried out

further experiments in the following year, but owing to war conditions the results of these were not published and they were subsequently handed to other workers.* The extension of the period of treatment to three hours, largely as a result of Ramsbottom's[17] work, formed the basis of the now universally practised "Hot Water Treatment" of narcissus bulbs as a control for bulb flies, *M. equestris* and *Eumerus* spp., and for bulb eelworm, *Anguillulina dipsaci*.

Some time before 1916 *Merodon equestris* was first observed in the United States of America. Metcalf[16] in that year recorded that adults were taken in some numbers at Bar Harbour, and expressed the fear that the range would continue to extend and that the insect would become a serious pest in the country. Larvae had already been recorded in New Jersey in 1915 by Weiss[21] and in British Columbia and Ontario as early as 1912 by Hewitt[9].

More recently numerous papers dealing with the fly have been published in both Europe and the United States of America. These papers indicate clearly that the pest has rapidly become a very serious menace to commercial stocks of narcissus wherever these are grown. No purpose would be served by mentioning the papers individually here, but reference to the more important of them will be made at relevant points in the present publication.

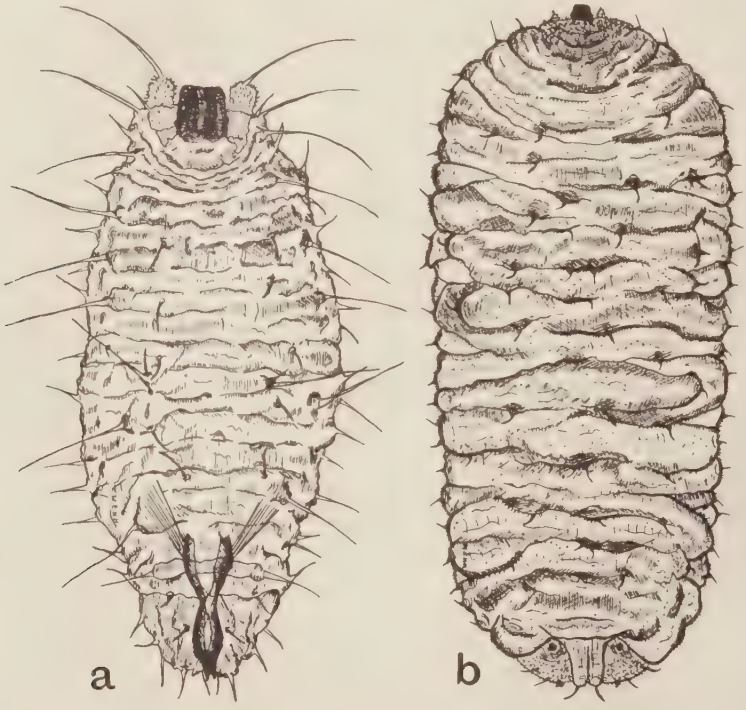


Fig. 1. *Merodon equestris*, F.: *a*, 1st instar larva (× 40); *b*, 4th instar larva (× 6·5).

Description of Stages of Merodon equestris.

Adult (Plate xxxix, figs. 1, 2).

A large conspicuous fly very pubescent and varying greatly in colour. Legs black, hind tibia of male humped inside just after middle and with a conspicuous

* Verbal communication by Mr. J. C. F. Fryer.

process at the tip, hind femora moderately thick. Length 12 mm. (a very full description of the adult fly is given by Verrall[23]).

Ovum (Plate xxxix, fig. 3).

Pearly white, faintly tinged with pink, surface of chorion finely and evenly tessellated. Shape elongate oval, tapering slightly at one end, length 1·6 mm.

Larva (fig. 1).

First instar. Dirty white, elongate oval, truncate posteriorly, posterior spiracular process and mandibular sclerites large and prominent, chestnut-brown in colour. Integument carrying rows of long prominent spinules, longest posteriorly. A prominent anal tubercle on either side of posterior spiracular process, each clothed densely with minute spines and carrying large spinules. Length 1·5–2 mm.

Second instar. Similar, except that the scattered spinules are less numerous and reduced in length to about one-third of those in first instar, and whole integument clothed with minute spinules. Length 2–5 mm.

Third instar. Similar, colour darker, scattered spinules still less prominent, posterior spiracular process relatively smaller. Large spinules on anal tubercles absent. Length 5·5–8·5 mm.

Fourth instar. Almost identical with previous one, except that spinules, anal tubercles, and posterior spiracular process, are again relatively smaller. Length 9·5–19 mm.

Puparium (Plate xxxix, fig. 4).

Tough and leathery, dark brown to black in colour, posterior spiracular process distinct and black, anterior spiracular processes protruded as a pair of horn-like projections on 8th to 10th day after formation. Length 12–14 mm.

Plants attacked.

The following list of bulbous-rooted plants in which *M. equestris* has been found is given by Fryer[6]:—Narcissus, Hyacinth, Tulip (rarely), *Amaryllis*, *Habranthus*, *Vallota*, *Galtonia*, *Scilla*, and *Leucojum*. With regard to attack upon narcissus Fryer presents further information thus, "A leading grower considers that hard bulbs of the *Narcissus maximus* and *N. spurius* type are least attacked, while the most susceptible are *N. poeticus* and *N. leedsii* varieties, and further, varieties with coloured cups are more susceptible than those without." The writer has been unable to obtain confirmation of this suggestion, in fact in the Tamar valley those growers who specialise in the colourless "Double white" frequently find this more seriously damaged than coloured cups such as "Ornatus" and "Horace." The critical factor is almost certainly the ease or difficulty with which the flies can approach the bulbs for oviposition. This in turn is determined largely by the condition of the soil and foliage of any given variety at the time of maximum oviposition and may vary as to variety or varieties from year to year.

After a lapse of 17 years additions to Fryer's list of food-plants are meagre. *Eurycles* can definitely be added, as can *Galanthus*, the wild snowdrop. In this latter plant the writer has found larvae in localities distant from cultivated bulbs of any kind. The attack on *Scilla nutans* recorded by Theobald seems to have been unusual, for many bulbs of this species have been examined, in districts where the fly abounded, without trace of injury being found.

With regard to the tulip it can be stated that oviposition on this plant is not infrequent. Larvae only enter the bulbs with comparative difficulty. Further, the activities of those which successfully effect an entry are likely to lead in a short time to a rapid bacterial and fungous decay of the bulbs. Entire destruction follows,

accompanied by premature death of the larvae from starvation. The writer has demonstrated that by periodically moving a larva on into a fresh tulip it can sometimes successfully be brought to maturity. At the same time in no observed case has a larva been found to complete its cycle in the tulip bulb in which it commenced feeding.

Symptoms of Attack.

A clear and detailed indication as to the nature of the injury caused, together with an account of larval behaviour, will be given subsequently. It will perhaps be of some assistance first to review the external symptoms of attack in order that identification of infested bulbs may be the easier, and for our purpose bulbs have been divided into three classes.

Newly lifted bulbs.

In normal commercial practice narcissus bulbs are lifted from the soil in July and early August, at which time the larvae are still small and have caused but little injury. Diagnosis of infested bulbs is therefore not very easy, unless they be submitted to the drastic measure of cutting in half with a knife. Nevertheless, it will be shown that a large percentage of the larvae enter the bulbs through the base plate and many infested bulbs can be detected at this early stage of attack if the base plates be carefully skimmed of all dead tissue with a sharp penknife. If a larva has entered the bulb a small rust-coloured spot, surrounding a tunnel a little smaller than a pin in diameter, is usually discernible in the base plate. Further, if the bulb is of sufficient value to warrant the trouble, judicious cutting and digging into the base with the penknife will frequently kill the larva before it has effected any very material injury.

Bulbs at planting time.

Planting usually takes place in September or early October, some four to six weeks after lifting. By this time the majority of the larvae will have tunnelled the centre of the bulbs to a considerable extent and will have entered their third instar.

With a little experience infested bulbs may usually be detected whilst handling at this stage. Such bulbs are somewhat softer than is normal, particularly in the region of the neck and can be rejected on this score with a very considerable degree of accuracy.

Symptoms in growing bulbs.

Assuming that an infested bulb has remained in the ground, or has inadvertently been planted, one of two things is likely to occur. If the bulb is small it may fail to shoot and be entirely destroyed. On the other hand, if the bulb be moderately large it is rarely killed outright, although the central growing point may be destroyed. Numbers of adventitious buds are likely to be formed in the axils of the individual bud-scales, as a result of the injuries sustained. Each of these buds in due course produces foliage, when, instead of a normal strong shoot appearing above ground, a circle of small leaves, appropriately termed " grass " by commercial growers, is seen. If the damage is a little less severe the infested bulb may itself send up weak, yellowish, and distorted foliage very reminiscent of attack by the bulb eelworm, *Anguillulina dipsaci*.

The above account refers in the main to symptoms of attack upon narcissus, the commercial crop most prone to extensive damage. It may, however, be taken as being generally applicable to attacks upon almost all of the food-plants previously listed.

Biology of the Fly.

Number of generations.

It can be accepted that there is not more than one generation each year, but certain writers have put forward the suggestion that larvae sometimes feed for two seasons before reaching maturity. Bliss[1] goes so far as to say that two forms or species occur, in one of which the larval life is completed in one year, the other having a two-year cycle. Bliss supports this statement by citing experiments in which bulbs were exposed to attack in one year and protected in the following year. In the spring of the third year adult flies emerged from the vicinity of these bulbs. In the writer's experience all larvae, without exception, mature in one year, an experience confirmed by Broadbent[2] working in America. It must therefore be assumed that the protection given by Bliss in the second season was incomplete. Bliss and others have doubtless been confused by the occasional occurrence of quite small larvae in the early months of the year. The presence and history of these will be discussed later.

Occurrence of adult flies.

The period during which adult flies are to be found is a relatively short one. Verrall[23] gives the dates 7th April to 28th June as the extreme limit of occurrence in England, but the April date refers to bred individuals and is therefore of little value. Bliss[1] gives 21st June as the latest date of capture in the field, with the exception of one individual taken on 5th July 1926. Lundbeck[14] gives 28th April to 3rd July as the limit in Denmark. Records kept by the writer for the past seven years provide the following dates of first appearance: 1925, 20th April; 1926, 10th May; 1927, 15th May; 1928, 8th May; 1929, 17th May; 1930, 10th May; 1931, 15th May. Dates of last appearance range from 27th June in 1925, to 9th July in 1931.

One point must be borne in mind, namely, that in forcing houses flies emerge much earlier than is normal. Numbers have been taken as early as 5th February in such situations, whilst one was taken on sallow in the open near Penzance on 18th March 1926. This individual had almost certainly escaped from a forcing house and taken advantage of the suitable weather conditions prevailing at that time. It is most unlikely that such "escapes" would meet with conditions suitable to oviposition so early in the year even if they mated and survived for their maximum life of three weeks.

We can say therefore that the normal flight period in England extends approximately from the first or second week in May until the end of June.

Longevity of adults.

Large numbers of flies have been bred in captivity and confined both in small cages and in insectaries in which they were provided with a close approximation to natural conditions. Females, whether fertilised or not, lived considerably longer than males. The shortest life of a female was 5 and the longest 24 days, the average being 17 days. Males varied from 6 to 18 days and averaged 11 days.

Proportion of sexes.

Many hundreds of flies were bred. Of the total 54·4% were females and 45·6% males. This ratio is of interest in that it agrees exactly with that found previously by Bliss[1] and is remarkable in that Bliss's figure refers to captured flies whilst the writer's concerns bred individuals. It was noted that approximately up to the end of May males were the more numerous sex, whilst during June females became increasingly predominant. This is due to two factors, the relatively earlier emergence of males and the longer life of the females.

Coloration of flies.

The adult flies exhibit striking variation as to colour. Some individuals are almost entirely tawny, some boldly banded with red, orange, and grey, and others entirely black, with the exception of the posterior abdominal segments which may be banded with red, orange, or grey.

Verrall[23] recognises the following varieties :—

equestris. Thorax with grey or tawny pubescence in front, but with a broad black fascia behind ; abdomen all fulvous except about the grey base ; scutellum with black or light pubescence.

narcissi. Thorax with entirely fulvous pubescence ; abdomen grey-haired.

transversalis. All grey-haired, except that the third abdominal segment is black-haired.

validus. Pubescence nearly all black except on the end of the abdomen.

Rondani[18] limits the variety *equestris* to those specimens in which the pubescence on the scutellum is light, placing the dark specimens as var. *bulborum*, which variety has been revived more recently by Bliss.[1]

The writer has collected and bred hundreds of the flies and the sorting of these by means of the varietal characters and the expression of the result in terms of flies per hundred provides the following data :—

TABLE I.

Var. *equestris*	♂ 7%	18%	Var. *transversalis*	♂ 0%
	♀ 11%			♀ 3%
Var. *bulborum*	♂ 23%	29%	Var. *validus*	♂ 0%
	♀ 6%			♀ 14%
Var. *narcissi*	♂ 16%	35%	Unplaced	♂ 0%
	♀ 19%			♀ 1%

In the experience of Bliss[1] and the writer all specimens falling within the var. *validus* are females, and we must therefore conclude that this particular coloration is a sex-linked character. The same appears to hold good for the far less common var. *transversalis*, although a few males placed as var. *narcissi* closely approximate to it. In fact var. *transversalis* is hardly distinct enough to warrant recognition. In the writer's series of flies only 3%, all females, have corresponded exactly with Verrall's description. If we consider the variety a good one, it is essential to erect yet another one into which 5% of flies of both sexes would fall. These flies are distinct from the typical var. *narcissi* in that they bear a definite bright tawny band transversely on the centre of the thorax. With these exceptions, only 1% of all flies cannot be placed in the varieties named above.

At the same time it must be realised that these varieties are purely arbitrary, in that a very considerable range of colouring is covered by each. It would be a simple matter to extend the number appreciably by narrowing the limits of each.

The writer is satisfied that the flies mate irrespective of colour, that the varieties are both cross and self fertile and that the progeny of a particular cross mating show a wide range of coloration. At this the matter must be left for the present, but a careful study of the varieties, conducted on a Mendelian basis, presents a fascinating problem. Such a study would be comparatively simple to carry out, for the flies may be bred with ease under controlled conditions.

Habits of Adult.

The fly is an exceedingly easy insect to rear and breed in confinement. Copulation and oviposition take place quite freely in small cages, provided that there is sufficient light. In this respect *Merodon* differs materially from *Eumerus* spp., in which it is difficult to induce oviposition even in a large insectary.

Emergence from pupa.

Emergence is effected through a large orifice at the anterior end of the pupa. A circular cap, containing on its inner surface the buccal armature of the larva, is broken away, the line of fracture being just behind the points at which the anterior spiracular processes protrude. The fly climbs any prominence near by and very soon becomes fully matured. Ninety per cent. of the flies emerge between the hours of 8 and 10.30 a.m. and none has been observed to emerge after mid-day. In newly emerged females the ovaries are small and the whole abdomen is packed with fatty globules, maturity not being arrived at for several days. Males are sexually mature 24 hours after emergence.

Feeding.

In the field flies may often be taken at flowers. Some preference is shown for those of various members of the order Compositae, notably the common dandelion. Flowering shrubs are visited and also, rather strangely, the large pink flowers of *Mesembryanthemum*, so abundant in the extreme south-western districts.

In captivity the flies thrive upon dilute sugar or honey solutions and also take water freely and frequently. Life is greatly shortened if no liquid be made available.

Response to sunlight and temperature.

One of the strongest arguments in support of the species being of southern origin, rather than indigenous to northern Europe, is the very marked inability to withstand unfavourable weather conditions for any length of time. Britain, Holland, and Denmark probably represent almost the extreme northern limit of the fly. Sweden imports annually large numbers of narcissus bulbs, particularly from Holland, and whilst *Merodon* is frequently bred from such imported bulbs, it does not appear to have become established in outdoor stocks, except perhaps in the extreme south.

The flies are never active on dull days, even if the temperature be as high as 70°F. In bright sunshine they may be quite sluggish at 68°F. if conditions be at all windy. Also there is an invariable tendency for flies to congregate in the warmest and most sheltered spots. Frequently numbers may be seen sunning themselves on convenient tree-trunks, fences, and banks.

Copulation.

This invariably takes place in bright sunshine accompanied by a high temperature. Conditions being suitable, flies of both sexes settle in sunny spots and call one another by means of a high-pitched vibration note which is clearly audible for some considerable distance. The note, which is produced apparently in the thoracic spiracles, is maintained for periods varying from a few seconds to two minutes, and at the conclusion short rapid darting flights are made. The male seizes the female by the thorax whilst in rapid flight and forces her to the ground. He then backs down her body and effects union, meanwhile clasping the thorax with the first pair of legs. The female sits motionless whilst the male, at frequent intervals, rapidly vibrates the wings and abdomen, again emitting the high-pitched call-note. At completion the male falls sideways and almost immediately flies away, the whole procedure occupying from 2–3 minutes.

Males are sexually mature 24 hours after emergence and females rarely copulate until the fourth day after emergence, the most usual day being the 6th or 7th, oviposition commencing 3–6 days later. To take a specific and typical case, a female

emerged on 8th June, copulated on 15th June, commenced to oviposit on 21st June and continued daily until death on 30th June.

Oviposition.

Dissections show that each female normally contains from 160 to 200 eggs. In Holland[24] the number laid is given as being from 60 to 100 per fly. It seems very unlikely that such numbers are usually laid by an individual.

In confinement and given every facility no fly has been induced to lay more than 15 eggs in a day or a total number of more than 81 eggs. The average figures obtained from 20 observed females was 5 eggs a day and a total number of 52. The average life of a female fly is 17 days, of which not more than 12 are available for egg-laying, the first 5 being occupied in reaching sexual maturity and mating. Therefore at the maximum rate of 15 eggs a day there is time for 180 to be laid. This figure is arrived at by ignoring entirely the weather factor. In practice, oviposition only takes place under sunny and warm conditions, and in May and June it is most unlikely that more than 2 days in every 3 will be suitable for the operation. This reduces our maximum to one of 120 eggs for an individual fly completing its allotted span. This figure, however, relates to a fly of exceptional performance. If we take the average number produced by the 20 observed females and treat it in a similar manner we find that a figure of the order of 40 eggs only is likely to be expected under normal weather conditions.

Fryer[7] has described the oviposition in some detail, and the writer cannot do better than include a very brief abstract of his observations, which were made on a narcissus bed. "The fly settles repeatedly on the foliage and ground, finally crawling to the centre of a plant. Here not infrequently is a hole $\frac{1}{4}$ inch or more in diameter left by the dying down of leaves and stem and extending below ground to the bulb itself. The fly backs down the hole and lays an egg on the earth forming the sides of the hole or less frequently on the leaves near the neck of the bulb. If the hole is blocked by earth or leaves the egg may be laid on the earth at the edge of the hole or under lumps of earth lying near. No eggs were found in the foliage above ground."

The writer has had ample opportunity for observing egg-laying, such observations, to a very large extent, bearing out those of Fryer. A point of difference is that eggs have frequently been observed to be deposited actually exposed on the soil surface and on dead leaves above ground. Such eggs rarely hatched, and even when they did so the chance of a larva successfully locating a bulb appeared to be singularly slight. Also, whenever the fly found it possible, eggs were actually tucked between the fractured ends of the outer scales surrounding the bulb neck. A point which Fryer[7] omitted to mention was the manner in which a fly preparing to oviposit extends the ovipositor. This is repeatedly extruded and withdrawn, the sensitive tip seeking actively for a suitable cranny in the soil, or space between the bulb-scales. When such a site is found the fly remains stationary until the egg is laid, a matter of some minutes.

In captivity a fly will lay 15 or 20 eggs on and around one bulb, but in the field one egg to a bulb is the normal procedure, although very occasionally an individual will lay 2, 3, or 4 consecutive eggs on one plant. It is no uncommon thing to find 4 or 5 eggs on one bulb, but almost invariably these have been laid by different flies at different times. Observation was kept on a number of bulbs collected in the field on each of which 3 or 4 eggs had been found. Without exception, eggs on individual bulbs hatched on widely different dates, clearly showing that they were not of the same age.

Egg mortality is high, ranging usually somewhere in the neighbourhood of 30% and rising in periods of adverse weather to nearly 90%. Dry hot weather shrivels up all eggs laid in exposed positions, whilst a spell of a few days of unduly wet conditions destroys nearly all eggs both above and below ground.

Published accounts provide very contradictory evidence as to the duration of the egg stage. In Holland[24] it is stated that the eggs hatch in 1 to 5 days. In the United States of America, Howard[10] gives 3 to 4 days, Weigall[20] 2 to 9 days, Wilcox,[22] in Oregon, 6 to 15 days, and Broadbent[2] states that over 2 years the average duration was 12 to 15 days.

In part these discrepancies may be due to varying climatic conditions, but the shortness of the periods given by some writers strongly suggest that their observations were not commenced upon newly laid eggs. The present writer's observations, carried out on several hundred eggs and extending over 5 years, show marked agreement with those of Broadbent.[2] All viable eggs have been found to hatch between the 10th and 15th day after being laid.

Habits of the Larva.

Entry into bulb.

The larva emerges from the egg through a ragged hole which it bites in the side in close proximity to the smaller end. When newly emerged, as described elsewhere, the larva is markedly dissimilar from the later instars and is exceedingly active. Its first objective is to gain entry into a bulb, and here again some uncertainty has existed as to the exact procedure followed. Weigall[20] states—"a larva was observed to work its way down the side of the bulb and apparently entered it at the base." Wilcox[22] says—"larvae usually enter the bulb through the base plate, this being the only part not protected by several layers of hard tough skin."

The basal region of the bulb is certainly the usual point of entry. A larva hatching from an egg placed near to, or actually upon, the side of the bulb invariably travels to the base plate and enters either at the point where the scale bases meet the base plate or through a depression in the plate itself left by a dead root. Larvae hatching from eggs laid between the scales usually work down between these scales until they reach the base plate, which they then enter through its dorsal surface. Occasionally the scales are too tightly packed together for the larva to progress between them, when entry may be made direct into a fleshy scale in the vicinity of the neck of the bulb.

Larval mortality.

Attention has already been directed to the high rate of mortality amongst the ova. Similarly, mortality of newly emerged larvae is considerable.

Fryer[7] states, "on several occasions 5 eggs were found round one plant and less frequently 3 and 1." This observation is in the experience of the writer accurate. Nevertheless, it is only very rarely that more than one larva is found in a bulb. Migration to a distant bulb of a newly emerged larva can in most cases be ruled out as being most unlikely, and we must therefore assume that, provided that 60% of the eggs hatch, numerous larvae never effect entry into a bulb. Further, up to 20% of bulbs in which entry holes have been made are found to contain minute dead larvae. At the same time, premature death is very rare once a larva has entered a bulb and survived the first few weeks.

Therefore, taking all factors into account, we may expect the progeny of a single female fly to number about twelve at maturity.

Larval behaviour in bulbs.

As we have seen, the newly hatched larva almost invariably enters the base plate of the bulb, either at the side or, more frequently, through the ventral surface. The entry tunnel is so minute that it can only be seen as a small rusty spot. The larva, once ensconced in the bulb, travels slowly through the base plate and for at least the first fortnight remains in this, feeding and growing very slowly and tunnelling usually in a horizontal plane.

At the conclusion of this preliminary period the larva commences to burrow upwards, the burrow usually assuming a rough spiral shape, and, deserting the base plate, enters the upper portion of the bulb. The growing point of the bulb is next devoured and rapid growth of the larva commences, it meanwhile working up through the bulb and forming a tunnel of ever increasing diameter. As the larva expands the tunnel becomes more and more tightly packed with frass, until the air-pocket on which the larva depends for respiration becomes exceedingly small. When matters arrive at this stage the larva descends through the bulb once more and feeds again in the base plate, through which it cuts a shaft of approximately the diameter of a lead pencil. During the later instars of the larval life the posterior spiracular process is actually protruded through this hole at the base of the bulb. The final exit from the bulb is usually made through this same aperture and not often through the neck, as has sometimes been stated, although before making its final exit the larva frequently journeys once more to the upper portions of the bulb for feeding purposes.

Migration from bulb to bulb.

Experimentally it can easily be demonstrated that a partly grown larva has no difficulty in entering a sound bulb. Such entry may be made by the larva cutting directly into the scales in a horizontal plane, or more usually at a point where scales and base plate meet.

In the field such a migration is sometimes necessitated by the larva exhausting entirely the resources of the bulb which it originally entered. This is particularly likely to happen when the attack is upon varieties of narcissus in which the bulb is small, *e.g.*, Ornatus and other Poeticus varieties, or when a larva enters a small offset in larger varieties such as Emperor or Soleil d'Or. Larvae appear unable to find their way to other bulbs through any considerable depth of soil, except by sheer chance, but in an established narcissus bed the bulbs lie closely approximated in clumps, when such migration is easily and not uncommonly effected.

Rate of larval growth.

One of the chief arguments put forward by persons maintaining that larvae may take two years to mature has been the established fact that quite small larvae are sometimes found in bulbs during the late winter and early spring months, it being assumed that such larvae could not reach maturity during the current season.

This assumption is incorrect, as is the somewhat similar one to the effect that flies oviposit on bulbs in store during August, this latter opinion being based upon the not uncommon occurrence of minute larvae in bulbs at planting time in October. Such bulbs have been out of the ground since, say, late July.

It can be stated quite definitely that the rate of growth varies from one individual to another over a very wide range. Accurate records of numbers of larvae have been kept and these provide interesting data.

The following table gives a very fair indication as to the order of variation commonly met with amongst larvae found in commercial samples of bulbs :—

TABLE II.

Year 1929–30	No. of larvae measured	Date measured	Maximum length	Minimum length	Average length
Bulbs lifted and removed to store 4th July, 1929	15	1.8.29	12 mm.	1.5 mm.	4.2 mm.
	20	1.9.29	15 mm.	4·0 mm.	8·6 mm.
	12	12.9.29	16 mm.	4·0 mm.	8·7 mm.
	11	7.10.29	15·2 mm.	3·5 mm.	10·6 mm.
	17	1.11.29	15·6 mm.	8·0 mm.	12·5 mm.
	12	10.2.30	19 mm.	14·0 mm.	16·8 mm.

Concentrating for a moment on comparatively small larvae, it is possible to show in another way the wide variation in the rate at which growth progresses. Numerous batches of bulbs were from time to time exposed to oviposition by *Merodon* flies for periods not exceeding one week in length, and then put aside until it was convenient to examine them. Ignoring completely all unduly large and small larvae and concerning ourselves entirely with larvae 4 mm. in length at the time of examination, we find the following variation in age.

TABLE III.

Batch of bulbs	Possible age of 4 mm. larvae.	
	Minimum	Maximum
A	13 days	15 days
B	18 ,,	27 ,,
C	36 ,,	38 ,,
D	38 ,,	47 ,,
E	44 ,,	53 ,,

We thus see that a larva may take anything from 13 to 53 days to reach a length of 4 mm., and there is no reason to think that these figures represent the limits of possibilities on this score.

As a final illustration, the performance of 3 individual larvae, progeny of 3 eggs laid by one adult on a single day, is of interest.

Each larva originally entered a separate bulb, the 3 bulbs being of one variety and of similar size. The larvae were periodically removed from their bulbs, measured, and returned to fresh bulbs, each thus being afforded equal opportunity of feeding and growth.

TABLE IV.

Eggs laid	Larvae A, B and C hatched and entered bulbs	Date of examination	Age of larvae	Length of larvae		
22.6.30	7.7.30	7.8.30	31 days	A. 6 mm.	B. 8 mm.	C. 4 mm.
		8.9.30	63 ,,	A. 14 mm.	B. 10 mm.	C. 8 mm.
		10.11.30	126 ,,	A. 15 mm.	B. 16 mm.	C. 8 mm.
		10.2.31	218 ,,	A. 17 mm.	B. 19 mm.	C. 14 mm.

Sufficient data have been presented in the tables above to show that larvae of greatly varying size are met with at any given time and that the size of a larva gives little or no indication as to its age. Thus, in Table III, larvae not more than 15 days old and larvae not less than 44 days old all measured 4 mm. in length. Again, in Table IV, one larva reached a length of 14 mm. in 63 days, whilst another was of the same length when 218 days old.

As indicating the extent to which this variation in rate of growth may occur it can be recorded that a single larva, to all appearances perfectly healthy and active, measuring only 5 mm. in length, was found in a bulb on 25th January 1929, the bulb having been in store since the previous August. The larva was transferred to a fresh bulb ; in 27 days its length increased to 8 mm., and a perfect though slightly undersized adult was produced on 6th June. Numerous other, though not quite such extreme, instances could be cited. A tendency has, however, been noticed for larvae whose development has been unduly retarded to be somewhat weakly and to form undersized pupae, from which adults not infrequently fail to emerge.

Reasons for variation in rate of growth.

Let us take first the less extreme variation as shown by the three larvae recorded in Table IV. At first glance the differences between the lengths of the larvae at the time of each examination are rather remarkable. It must be borne in mind that the larval skin is cast at intervals, and that prior to ecdysis growth is slow, whilst immediately after it becomes for a time more rapid. The larval stages of *Merodon equestris* occupy roughly 300 days, and during this period the skin is probably cast four times only. It is therefore only to be expected that a group of larvae hatched at any given time will show some variation, extending even into weeks, as to the date at which ecdysis takes place. The criterion as to the date of ecdysis is the colour of the posterior spiracular process; this is invariably of a light chestnut colour for several days after a moult.

Whilst these observations account satisfactorily for the variation in size of larvae over fairly wide limits, they do not account for the occasional occurrence of small second-instar larvae in late winter and early spring months, and we must look elsewhere for the explanation. Two observations assist us on this score, the first that large fleshy bulbs always contain large, well nourished larvae, and the second that markedly undersized larvae usually occur in partly desiccated bulbs, *i.e.*, bulbs which have been out of the ground for an abnormally long period, or which have been stored under excessively dry conditions. When, as happens very occasionally, such larvae are found in a perfectly normal bulb, they are always in the base plate. Larvae feeding in bulbs kept dry in the laboratory grow more slowly than larvae feeding in bulbs planted in soil in the insectary and, in fact, have sometimes only been kept successfully by the occasional squirting of small quantities of water into their burrow.

With regard to the occurrence of small larvae in the base plates, similar reasons hold good. It has been observed that all larvae grow slowly until such time as they become ensconced in the bulb scales, which they eventually reach by boring through the dorsal surface of the base plate. Sometimes larvae fail to penetrate the scales until long after the normal time for so doing. Again, occasionally the base plate is particularly hard, with resultant unusually slow progress on the part of the larva.

We are thus forced to the conclusion that undue retardation of growth is brought about by a difficulty in obtaining access to the ample supplies of food present in the fleshy scale portion of a narcissus bulb. Definite proof of this is apparently provided by an experiment carried out by the writer in which numbers of newly emerged larvae were fed exclusively on base plates removed from bulbs. These larvae all fed and grew very slowly in spite of ample supplies of fresh base plate tissue being provided. Conversely, larvae fed from the time of hatching on bulb scales alone progressed rapidly.

Departure of larvae from bulbs.

Expressed in round figures a normal larva remains in a bulb for 300 days. Exit from the bulb is usually made through the hole previously cut through the base plate, at least 95% of all larvae leaving the bulb through this hole; approximately 1% emerge through the neck of the bulb and the remaining 4% through some point at the side. In view of the considerable length of the larval life, and the variation in size amongst larvae at any given time during the period, the date of migration from the bulbs is singularly constant and varies very little from season to season. In the extreme south-west of England a few larvae leave in February and the migration commences generally during the first week in March. By mid-March 50% of the larvae have left, and only 3% remain in the bulbs by the end of the first week in April. Full records of dates are not available for other districts, but there are indications that in the eastern counties migration is approximately 14 days later.

Pupal Stage.

Pupation.

Having left the bulb the larva travels slowly through the soil, leaving in its wake a definite tunnel of about the thickness of a lead-pencil. In any but very sandy soils this tunnel can frequently be found and the larva traced to the end of it. The tunnel varies in length from 6 in. to over 2 ft. and terminates usually at surface level, where pupation takes place, with the anterior end of the pupa flush with the soil surface, from 2 to 10 days after the bulb is vacated.

Length of pupal period.

As is the case with many other Syrphid flies, the anterior spiracular processes are not protruded until some time after the pupa is formed. The protrusion usually takes place on the 8th day after pupation, but may be delayed until the 10th day. Broadbent[2] gives 33–61 days as the extreme range of length of the total pupal period. In the writer's experience the length of this stage has shown marked consistency, varying only between 35 and 40 days. At the same time it seems highly probable that it can be prolonged for a further 10 or even 20 days, it being impossible otherwise to account for the total period of time elapsing between the earliest vacation of the bulbs and the appearance of the first flies.

Rate of Increase of the Fly.

In an earlier paragraph it was stated that, at maturity, the progeny of a single fly may be expected to number approximately 12. The figure was arrived at by taking the average performances of some hundreds of flies for several years, the flies being confined under conditions closely approximated to those found in the field.

The determining factor which permits of a material increase in the fly population annually is the abundance and accessibility of suitable material on which to oviposit. Critical field observations have been carried out in Devon and Cornwall on commercial narcissus plantations. Certain of these plantations were newly established in comparatively isolated areas at the time when observations were commenced. The rate of increase in fly populations on such holdings, over a number of years, has shown marked similarity to that rate which has been estimated from the breeding work.

An increase of this order may be expected to continue for a number of consecutive years until the advent of a season markedly adverse to successful oviposition by the fly. Such a season would appear to occur once in every 4 or 5 years and is marked in the year following by a very decided set-back, the population remaining stationary or even showing a slight decline.

Parasites.

One reference to the occurrence of a parasite of *M. equestris* has been met with in the literature, namely that of Cushman,[4] who records *Rhembobius* (*Phygadeuon*) *abdominalis*, Prov., from *M. equestris* in Washington in 1929. In the many hundreds of flies which have emerged in captivity during the present investigation no case of parasitism has been observed. A few undetermined Tachinid flies have appeared amongst flies bred from bulky consignments of infested bulbs. In no case could these be induced to oviposit on or near larvae, and they were very possibly associated with some other insects frequently found in such consignments.

Control Measures.

At the outset it was made clear that, despite the accumulation of a very considerable quantity of literature regarding the fly, progress towards the evolution

of a satisfactory and permanent check to its ravages has been in many ways disappointingly slow.

It is clear, from the very nature of the crops attacked and the manner in which attacks take place, that the pest is unlikely to prove an easy one to combat. The position is further complicated by the absolute necessity of taking into consideration other, and equally serious, enemies of bulbous plants which also must be controlled. Again, whilst bulbs in general are tolerant of much during dormancy, it is desirable for their well-being that they are afforded a minimum of disturbance when growing, over periods of time extending into two or more years.

Therefore it is unlikely that any one specific method of control will be applicable in every case. A combination of methods, having due regard for all attendant circumstances, and extending over several seasons, will be most likely to achieve the desired end.

It is proposed to review very briefly the known and accepted control methods already practised and to make further suggestions where possible. The account will conclude with information regarding the use of a poison bait spray against the adult flies, a subject on which a preliminary publication[12] has been made recently.

Cultural methods.

The suggestion that flies might be deterred from egg-laying by a comparatively simple expedient was made as long ago as 1915 by Fryer.[8] This consisted of filling in all holes and crevices present in the soil on beds of bulbs during the period when oviposition was likely to take place. In a more recent publication, concerned primarily with the Lesser Bulb Flies, *Eumerus* spp., the writer[11] paid particular attention to control by means of cultural operations. It was shown that a high measure of success accompanied careful attention to such methods. Indeed so satisfactory are the results obtained by these means that certain of the operations there suggested have become routine measures amongst the more progressive bulb and flower growers.

The measures comprise surface cultivation at the correct season, earthing up and occasionally cutting of foliage, early removal of lifted bulbs to cover, and the use of decoy heaps of valueless bulbs for the attraction of ovipositing flies. Whilst these measures are of undoubted value, factors discussed elsewhere[12] do not permit of their invariably providing an efficient control of the fly when practised alone. It is essential that direct action also be taken against the fly itself, either in the adult or immature stages. Before discussing these, attention must be directed to an additional safeguard which may be practised with benefit in certain cases.

Covering bulbs during growth.

Observation has shown that ovipositing flies are very loath to enter cover, however primitive this may be. It is clearly out of the question to cover large commercial stocks of bulbs whilst in growth, but most large growers possess small beds of bulbs of considerable value. The bulbs may be small stocks of new and rare varieties or material saved for hybridising purposes. Such beds may conveniently and cheaply be covered, during the ovipositing season, by means of horizontal screens of butter muslin or hessian, stretched above the beds at a height of 4 feet from the ground. If the bulb beds are not of greater width than say 5 feet, ample light and air are provided for the plants at the stage of growth normal to the season of the year at which protection is required.

Removal and destruction of infested bulbs.

An account has already been given of the means by which bulbs containing larvae may be detected. We are here concerned with those placed in the last category, namely growing bulbs which in the spring throw up weak or abnormal foliage owing

to the presence of a fully developed larva in their centre. Certain commercial growers make a practice annually of sending teams of workers round their beds for the purpose of rogueing out and destroying such obviously affected bulbs. Many larvae are certainly collected in this manner, one grower accounting for over 5,000 in the spring of 1931. Nevertheless in the writer's opinion the procedure is of little or no value on the average bulb farm. Firstly it requires a very keen eye and exact knowledge to detect a reasonably high percentage of such bulbs. Secondly migration of larvae from the bulbs often commences before the symptoms are very obvious, with the result that before the work of rogueing can be anything like completed a high proportion of the bulbs detected and lifted will already have been vacated by the larvae. As against this, on one holding the workers have become so proficient that if the bulb is vacated they search for the larval burrow in the soil and finally, in many cases, collect the pupa.

The writer has a very considerable acquaintance with the field aspect of bulb culture, and it can be stated with confidence that however well such work be done it is unlikely that 50% of the larvae will be accounted for. The remaining 50% are ample in numbers to give rise to an exceedingly severe infestation in the following season.

Swatting of adult flies.

Many growers in the West of England expend much time and energy in destroying adult flies by means of an orthodox fly swat or a home-made apparatus constructed on similar lines with the addition of a long handle. This practice cannot be recommended for two reasons: firstly, the number of flies accounted for is exceedingly small; secondly, indiscriminate swatting usually commences with vigour too early in the year and the "bag" consists very largely, if not entirely, of harmless or beneficial flies, *Eristalis tenax* being the principal victim.

Hot water treatment of bulbs.

The standard hot water treatment of narcissus bulbs is directed primarily against the bulb eelworm, *Anguillulina dipsaci*, and consists of steeping the bulbs whilst dormant in water heated to 110°F. for three hours.

Such treatment is fatal to *Merodon* larvae, as indeed is one hour's immersion at that temperature, but for several very good reasons it is not expedient to treat bulbs in this manner more often than once in every two or three years. After treatment bulbs are usually planted down for two or more years, during which time a very serious reinfestation is liable to occur.

Submersion of infested bulbs in water containing chemicals.

No very promising results have so far attended work on these lines. A varying percentage of larvae can always be killed, even by prolonged immersion in water alone, but the presence of air pockets and the naturally impervious nature of a bulb mitigate against the obtaining of a satisfactorily high rate of mortality, even when using comparatively concentrated solutions of such substances as nicotine or formaldehyde.

Recent experiments, in which air was withdrawn from the bulbs during immersion in the above liquids, by means of a partial vacuum, have shown more promise of success. It is proposed to continue work on these lines with the view principally of endeavouring to obtain a substitute for the not entirely satisfactory hot-water treatment.

Fumigation of bulbs.

(*a*) Paradichlorbenzene.

As previously described[11] box fumigation of dormant bulbs with this material affords a complete control for bulb fly larvae. It is a method worthy of more

extended use than it is given at present, for it is entirely non-injurious to the bulbs. Provided that a suitable chamber is constructed, bulbs may be placed directly in this in their storage trays, thus avoiding additional handling. 4 oz. of paradichlorbenzene should be used for every cubic foot of space in the container, as originally suggested by Stenton,[19] and the fumigation should be of 120 hours duration. The initial cost of paradichlorbenzene is considerable, but the original charge will remain effective for a large number of batches of bulbs, and in fact will require but small additions during the treating season, provided that reasonable care is taken in keeping the chamber closed except when filling and removing bulbs. The only point to which very special attention should be paid is to ensure that the bulbs are not permitted to heat or sweat during fumigation. The danger of this occurring is almost entirely obviated if care is taken that the bulbs are dry when placed in the chamber.

(*b*) Carbon disulphide.

Fumigation of dormant bulbs with this substance has been carried out in the United States. Mackie[15] in 1922 killed all Lesser Bulb Fly larvae and therefore presumably *Merodon*, which is less resistant, by vacuum fumigation, 2 lb. carbon disulphide per 100 cubic feet for a period of one hour having been used. Mackie reported that bulbs were uninjured by the treatment, but that longer exposure usually resulted in damage. That the method cannot be considered very successful may be judged from the subsequent U.S. Quarantine order in which fumigation of bulbs with calcium cyanide was officially authorised.

(*c*) Calcium cyanide.

Some years ago the writer carried out a few preliminary tests of this fumigant. The experiments were not very extensive but sufficient evidence was obtained to state that, with care, bulb fly larvae may be killed without injury to the bulb. It was not found possible to devise a dose lethal to bulb eelworm without at the same time injuring the bulb. Doucette[5] in 1924 carried out experiments with calcium cyanide fumigation of bulbs, being concerned first with aphides occurring on Iris in store and extending the work to include *Merodon* larvae in Narcissus in 1926. Cole[3] carried on the work and now definitely recommends fumigation on the lines suggested in the U.S. Quarantine order as being reasonably satisfactory. Bulbs should be fumigated in an air-tight box at a temperature between 60 and 90°F. The dosage being 12 oz. of calcium cyanide (granular) per 100 cubic feet of space and the exposure 4 hours. It is not yet certain whether such fumigation will kill all first instar *Merodon* larvae.

Deterrents to oviposition.

As already recorded[12] no great success has attended the use of deterrent material for the purpose of keeping flies away from beds during the oviposition season. Such substances as paraffin emulsion sprays or broadcast dressings of naphthalene have been used.

Further field trials with naphthalene and proprietary soil fumigants have been carried out in various parts of the country during the past season. These have, with a few exceptions, furnished further proof that such methods are usually too transitory in their action to afford any material benefit. It must, however, be recorded that in one instance repeated surface dressings of crude naphthalene, each dressing consisting of 3 cwt. an acre, appeared to effect a very satisfactory measure of relief from infestation.

Poison-bait sprays.

The suggestion that a poison-bait spray might possibly afford a means of destroying the adult flies emanated originally from Holland.[24] It was, however, a suggestion only and no trials appear to have been carried out there with a view to testing its efficacy.

The writer first commenced field experiments with poison baits in 1926, as an outcome of the observation that in captivity the flies fed freely upon solutions of sugar in water. A preliminary publication, recording the results obtained up to 1930 was published recently,[12] and there is no need to recapitulate the evidence then set out. Sufficient to say that two sprays were tentatively put forward as showing promise of success. Subsequent work has shown that one of them, comprising a mixture of sodium arsenite, sugar, glycerine, and water, proved its superiority and has now been adopted definitely.

The preliminary publication referred to above was concerned largely with comparatively small scale work. During the past season trials have been conducted on a more extensive basis, and the bait used throughout the trials was standardised, being composed as follows :—

Material	Cost
	s. d.
Sodium arsenite 4 oz.	0 5
Glycerine (crude) 1 lb.	0 8
Sugar (white cane) 2 lb.	0 5
Water 4 gall.	—
	1 6

The bait was applied by means of standard knapsack sprayers of various well-known makes, applications being made, as far as possible, weekly throughout the ovipositing season. In the year under consideration this lasted roughly from 20th May to 1st July.

It will be appreciated that a critical examination of results obtained from such trials is difficult if not impossible to make. At the same time some 200 acres of growing bulbs were treated. Definite information was obtained as to the practicability of the procedure and cost involved. Bulbs were examined on subsequently lifting them and every indication of a diminution in degree of infestation was obtained. For convenience the trials will be discussed in three sections.

(*a*) A baiting scheme inaugurated at the Western Commercial Show, Penzance, in March 1931.

This scheme was financed from the Show Funds, growers participating in the scheme agreeing to pay 5s. an acre of bulbs baited, the work being carried out by officials of the Cornwall County Council. Some 70 acres in the vicinity of Penzance were baited under this scheme.

The work was thoroughly carried out and records show that an average quantity of 6 gallons of spray fluid was used to an acre. Including time occupied in mixing the ingredients, the average rate of spraying was one acre an hour. The final figure arrived at, estimating wages at 1s. an hour and allowing 3d. an acre for the loan of the spraying machines gives a cost of 3s. 6d. an acre for a single spraying or 17s. 6d. an acre for the 5 sprayings considered needful during the season. This figure is ridiculously low when one considers the large capital sum represented by the value of 1 acre of bulbs of even the commonest of commercial varieties.

The writer is indebted to Mr. Abbiss, Horticultural Superintendent for Cornwall, for the following information as to the result of these trials :—

> " Numbers of dead flies were found after treatment and there appeared to be a decrease in grub injury in the treated areas. The fact that some growers outside the areas, who did not bait, have had a very bad infestation and lost quantities of their bulbs seems to emphasise the value of the treatment."

(*b*) Baiting by individual growers in the West of England.

About 100 acres were treated in places throughout Cornwall and at least one centre in Devon. In these cases it has not proved possible to obtain accurate figures as to the cost of the operations, principally owing to the writer's removal from the West of England. At the same time numbers of these growers have expressed satisfaction as to the results obtained, as judged by the condition of bulbs lifted and examined subsequently, and have signified their intention of repeating the baiting annually.

(*c*) Baiting carried out by a grower of comparatively valuable stocks of bulbs in S.E. England.

An account of this work must be included as it is in very marked contrast with the methods adopted in the other instances.

As a commencement, very careful attention was paid to the response to weather conditions exhibited by *Merodon*, and spraying was only carried out between 10 a.m. and 3.30 p.m. on warm and sunny days. Again, the first spraying was followed immediately by a second on account of a very heavy thunderstorm intervening, which entirely washed away the first application. Seven complete and a partial eighth spraying were made instead of the five recommended, the first commencing on 26th May and the last concluding on 7th July.

A one gallon Holder-Harriden Sprayer was used. It was found that only one acre a day of 5½ hours was covered in a manner satisfactory to the grower, as opposed to one acre an hour in previous cases. Again, an average of 16 gallons an acre of fluid was used instead of the 6 gallons previously or the 8 gallons originally suggested by the writer. The grower in question maintains that the extra cost per acre involved is negligible when considering the value of the crop and rightly states that it is impossible to wet all foliage with a smaller quantity of fluid.

As regards the result obtained at this centre, again exact figures are unobtainable, but the grower reports "This lifting season has been definitely noticeable for apparent lack of *Merodon* infested bulbs."

Discussion of results.

Sufficient evidence has been produced to indicate that poison-bait spraying of bulbs is not an excessively costly procedure and that such spraying appears to produce a marked diminution of bulb fly attack. It further shows that the number of sprayings and rate of application has not been entirely standardised.

In the opinion of the writer, 6 gallons an acre is a distinctly low rate to work on, although it must be realised that no effort need be made to cover every portion of foliage. The object in view is to obtain a wide distribution of the bait in order that flies are likely to find it by chance when alighting. In the case of growers of smaller quantities of highly valuable stocks the use of 16 gallons an acre, with an increased number of applications is probably economically sound. For the general bulb farmer it is recommended that the 6 gallon rate used in 1931 be increased to the 8 gallons originally recommended, or even to 10 gallons an acre.

In the opinion of the writer the use of a poison-bait spray containing sodium arsenite against *Merodon equestris* will provide a high measure of control. At the same time until further evidence be forthcoming it would be unwise to consider it sufficiently effective unless used in combination with control methods previously advocated.

Methods recommended for obtaining control of the fly.

1. Bulbs should be subjected to the "hot water treatment" whenever they are lifted. In practice this will be every second or third year and will ensure complete freedom from infestation in newly planted stocks.

2. In the subsequent season or seasons when the bulbs remain in the ground special attention should be paid to surface cultivation of the soil during the whole of the period during which ovipositing flies are likely to be present.

3. Periodic spraying with the poison-bait spray should be resorted to, whether the bulbs be due for lifting or not. Sprayings should be made at approximately weekly intervals, the exact dates being determined by the weather conditions prevailing.

The sprayings should commence and terminate at approximately the times previously mentioned, *viz.*, the second week in May and the last week in June, or first week in July.

4. In certain cases, *e.g.*, where lifted bulbs are to be forced and are known to be free from bulb eelworm, fumigation might perhaps with advantage be substituted for the hot water treatment.

Summary.

1. The history of the occurrence of *Merodon equestris* in various countries is related and a list of known food-plants given.

2. The immature stages of the fly are described in detail.

3. The biology of the fly is fully discussed and additions made to our knowledge regarding it.

4. Control measures are reviewed and additional information is given, particularly with reference to the use of a poison-bait spray against the adult flies.

5. Recommendations are made as to the most satisfactory combination of methods to use for the purpose of obtaining control of the fly under field conditions.

6. A list of literature cited is given.

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Fig. 1. *Merodon equestris*, adult male, x 4.



Fig. 3. *Merodon equestris*, ova on leaf, x 2·8



Fig. 2. *Merodon equestris*, adult female, x 4.



Fig. 4. *Merodon equestris*, puparium, x 3·8.

SODIUM FLUOSILICATE AS A POISON AGAINST THE HOPPERS OF *LOCUSTA MIGRATORIA MIGRATORIOIDES*, R. & F., IN NIGERIA.

By F. D. Golding, M.A., F.E.S.

Introduction.

In December 1929, swarms of the Migratory Locust, *Locusta m. migratorioides*, R. & F., entered the south-western corner of Nigeria from Dahomey and rapidly spread throughout the colony. Between the end of March and mid-July 1930, hopper bands -derived from these swarms—occurred in the Oyo and Abeokuta Provinces in the south-west and in all of the eleven Northern Provinces. There was a second breeding season from mid-August to the end of December 1930, in the Northern Provinces and, in 1931, two more generations of hoppers occurred in the north, each generation being a few weeks later than the corresponding one in the previous year.

In 1930, there was a considerable prejudice in some of the Northern Provinces against control measures involving the use of arsenical preparations, as it was feared that fatalities would occur on account of the popularity of locusts as an article of diet amongst most of the Nigerian tribes, a number of which regard even hoppers as a culinary delicacy. Control was therefore largely restricted to such primitive methods as trenching, trapping and even beating, although a few months after the commencement of the campaign the poisoned bait method was introduced into the Zaria and Bornu Provinces by the writer's colleague, Mr. O. B. Lean. In the following year bait poisoned with sodium arsenite was used on a large scale throughout the Northern Provinces ; in neither year was there a fatality amongst the natives, nor was the loss of domesticated animals considerable. In spite of the almost complete immunity from accident experienced in Nigeria to date, there is no doubt that the use of sodium arsenite as a locust poison is undesirable on account of the potential danger to man and stock in a country inhabited principally by uneducated natives and with a relatively small number of Europeans available for the supervision of the manufacture and application of the bait.

Late in 1930 it came to the notice of the Nigerian Agricultural Department that sodium fluosilicate was being utilised against the Desert Locust, *Schistocerca gregaria*, Forsk., in India. One cwt. of this substance was obtained from England and the writer carried out a number of tests against the hoppers of *L. m. migratorioides* in various localities during the two campaigns in 1931 ; the present paper is devoted to an account of the results of these tests and to a discussion of various matters concerned with the use of poisoned bait against locust hoppers.

Field Tests of Sodium Fluosilicate.

Fleming[3] states that the approximate amount of sodium fluosilicate (Na_2SiF_6) which will dissolve in 1,000 parts of water at room temperature is 7·14 parts. As commercial fluosilicate is known to vary considerably in its composition the writer carried out two solubility tests with the poison received from England ; it was found that approximately 6·80 parts per 1,000 parts of water were dissolved at 24·5°C. and about 7·03 parts at 28°C. The standard method of preparing arsenical bait in Nigeria is to dissolve 12 oz. of sodium arsenite in 8 gallons of water and then to steep the carrier (usually weighing about 30 lb.) in this solution. Richards[11] has recommended that one part of sodium fluosilicate should be mixed with 40 parts of dry bran, the ratio of poison to carrier being identical with that used in Nigeria

for sodium arsenite, viz. 1 : 40. It is obvious that if the " wet " method of bait preparation is employed for fluosilicate, only about 9 oz. of the poison would be dissolved by 8 gallons of water, while about 3 oz. would remain undissolved. As the wet method had been carefully explained to the numerous Europeans in charge of arsenical bait factories, it was hoped to be able to utilise a similar method of manufacture should sodium fluosilicate be substituted for sodium arsenite. Accordingly the writer employed the wet method of manufacture in his first trial of fluosilicate, but it was found that the method was laborious and unsuitable for general use on account of the need for continual stirring during the addition of the carrier to the water containing poison both in solution and suspension ; thus after the first trial the dry method of preparation was always employed. It was thought advisable, in the interests of economy, to determine whether it is necessary to add an attractant to bait containing fluosilicate ; one of the advantages of sodium fluosilicate over sodium arsenite is its comparatively low cost, but this advantage would be vitiated if an attractant were essential.

(*a*) Trial near Bauchi, 20th to 23rd May 1931.

On 18th May, about 30 lb. of each of the following baits were prepared by the wet method described above :—12 oz. sodium arsenite, 8 gallons water, 30 lb. guinea-corn bran ; and 12 oz. sodium fluosilicate, 8 gallons water, 30 lb. guinea-corn bran.

Both baits were sun-dried for 3½ hours on the 18th and for 6 hours on the 19th, because the drying process reduces transport costs to the field and renders the bait easier to handle ; before use against hoppers water is added at the rate of 5–6 gallons to 30 lb. of bait.

Only three bands of hoppers were available, two in the second instar and one in the first ; usually baiting is not carried out until the second instar is reached. The results of the experiment are tabulated below :—

TABLE I.

Area of band and instar	Type of bait	Approximate percentage killed in 72 hours	Time and rate of application
One acre ; 2nd instar	Arsenite ...	98	6.20 a.m. ; 30 lb. an acre
½ acre ; 2nd instar	Fluosilicate ...	5	7 a.m. ; 30 lb. an acre
250 sq. yards ; 1st instar	Fluosilicate ...	5	6.45 a.m. ; 30 lb. an acre

The differences in the times of application were insignificant as the temperature was low and the hoppers were comatose until about 7.30 a.m. Much valuable experience was gained from this necessarily small scale preliminary trial. The principal difficulty encountered was the segregation of the treated bands from other small bands which appeared unexpectedly during the three days following baiting. It was found that it was essential to watch each treated band throughout the day and to have men available for driving off or destroying untreated bands in the vicinity.

(*b*) Trial near Zaria, 13th to 19th June 1931.

Hopper bands were more numerous at Zaria than at Bauchi, but the majority of them were very small. It was decided to add common salt to some of the fluosilicate bait and to utilise the dry method of manufacture. Two types of bait were prepared, the first consisting of 30 lb. of sawdust mixed dry with 12 oz. of sodium fluosilicate, and the second of 30 lb. of sawdust mixed dry with 12 oz. of sodium fluosilicate and then sprinkled with a saturated solution of 12 oz. of common salt

in water. After sprinkling the salt solution over the bait, the whole was thoroughly mixed ; this is the method of preparation advocated by Richards.[11] Before application both baits were moistened by the addition of water at the rate of 5 gallons to 30 lb. of bait.

TABLE II.

Area of band and instar	Type of bait	Approximate percentage killed in varying period	Time and rate of application
60 sq. yds. ; 4th instar	Fluosilicate plus salt	50 (after 17 hours) 80 (after 24 hours) 98 (after 48 hours)	6.30 p.m. ; 160 lb. an acre
As above	As above ...	Results identical with above	6.40 p.m. ; 160 lb. an acre
60 sq. yds. ; mostly 4th instar, a few 5th instar	Fluosilicate without salt	50 (after 17 hours) 75 (after 22 hours) 85 (after 48 hours)	7 p.m. ; 160 lb. an acre
100 sq. yds. ; 4th instar	As above ...	95 (after 29 hours) 100 (after 48 hours)	7.50 a.m. ; 100 lb. an acre

It will be seen that the results shown in Table II indicated that it is unnecessary to add salt to fluosilicate bait when sawdust is utilised as a carrier.

(*c*) Trial of chopped hay and sodium fluosilicate.

As described in a later section of this paper, the writer found that chopped hay was a satisfactory carrier when impregnated with sodium arsenite at the rate of 12 oz. to 28 lb. of carrier ; as it was thought that this readily obtainable carrier might be used in considerable quantities in the future, it was determined to prepare and test baits consisting of chopped hay and sodium fluosilicate. The bait was prepared by mixing chopped hay and fluosilicate at the rate of 30 lb. of carrier to 12 oz. of poison ; before use 6 gallons of water were added to 30 lb. of bait. Between 8 and 8.40 a.m. on 27th June this bait was applied at the rate of 80 lb. an acre to three bands of fifth instar hoppers with areas of 100, 300 and 1,200 square yards, respectively. The hoppers were lethargic and the final ecdysis commenced on the day after the bait was applied ; about 40% of the hoppers died in spite of the unsatisfactory conditions for baiting. No further opportunities for experimental baiting occurred until the end of July, when the writer found a band of second instar hoppers near N'Guru, in the north-western corner of the Bornu Province. This band, which covered an area of about 200 square yards, was baited at 7.35 a.m. on 27th July at the rate of 75 lb. an acre with a bait consisting of 30 lb. of chopped hay to 16 oz. of sodium fluosilicate. The following percentages of hoppers had died at examinations 8, 24, 32 and 48 hours respectively after the application of the bait : 25, 50, 75 and 86. It will be seen that the addition of salt to fluosilicate-hay bait does not appear to be necessary.

(*d*) Trial near Mongonu, 22nd September to 3rd October 1931.

The principal carrier utilised in the Chad area is guinea-corn bran, which had given unsatisfactory results in the preliminary trial at Bauchi four months earlier. It was decided to repeat the Bauchi experiment, but to utilise the more convenient dry method of manufacture, and 1,845 lb. of bran were mixed with sodium fluosilicate at the rate of 12 oz. of poison to 30 lb. of carrier.

The following table shows the results of the trial of this bait :—

TABLE III.

Area of band and instar	Approximate per cent. killed in varying periods	Time and rate of application
3 acres ; 2nd instar	7 (after 24 hours) 20 (after 48 hours)	6.30 a.m. ; 80 lb. an acre
7 acres ; 2nd instar	15 (after 48 hours)	6.15 a.m. ; 129 lb. an acre
900 sq. yds. ; 3rd instar	None died	6.15 a.m. ; 200 lb. an acre
2,660 sq. yds. ; 3rd instar	None died	6.45 a.m. ; 295 lb. an acre
3 acres ; 3rd instar	None died	6.15 a.m. ; 164 lb. an acre

It is possible that in the 3rd and 4th experiments the bands were baited too soon after the completion of ecdysis. It was not found practicable to observe whether the hoppers fed upon the bait, as owing to high temperatures in the early morning, they were readily disturbed and were liable to move off the baited area if an observer approached near enough to be able to see whether they were feeding.

It was decided to incorporate common salt in the fluosilicate bait for further trials, and 1,542 lb. of bait, consisting of guinea-corn bran, sodium fluosilicate and common salt at the following rates : 30 lb., 12 oz., 12 oz., were prepared.

Table IV shows the results obtained with salted bait.

TABLE IV.

Area of band and instar	Approximate per cent. killed in varying periods	Time and rate of application
2,600 sq. yds. ; 3rd instar	Very few ; band dispersed after being baited	6 a.m. ; 260 lb. an acre
10 acres ; 3rd instar	60 (after 48 hours)	6.30 a.m. ; 160 lb. an acre, (only 6 acres baited)
3 acres ; 3rd instar	70 (after 72 hours)	6.30 a.m. ; 144 lb. an acre

In the 2nd experiment the bait was applied to the northern section of the band, as from previous observations it was thought probable that the band would move in a northerly direction ; this assumption proved to be correct and the whole band passed over the baited area. It was very difficult to assess the proportion of hoppers killed, since after baiting the band became dispersed over a very large area, and it was noted that hoppers were still dying five days after the bait was applied ; it is thought the percentage figures in the 2nd and 3rd experiments are rather too low.

On the conclusion of the fluosilicate baiting the writer carried out a number of tests with ordinary arsenical bait (30 lb. guinea-corn bran, 12 oz. sodium arsenite), and in no case did the kill exceed 50%. It should be mentioned that baiting is seldom so effective in the Bornu Province as in other parts of the country, probably on account of high ground temperatures in the early morning. In one test with arsenical bait three bands were baited at 6.20, 6.50 and 7.20 a.m. respectively and it was found that the percentage of hoppers killed was greatest in the first band baited and least in the last. Salted fluosilicate bait was more effective than arsenical bait applied at the same time in the morning on the following day.

(*e*) Trials in the Zaria Province in May and July 1931.

Two officers of the Agricultural Department kindly carried out tests with sodium fluosilicate baits, and their results may be summarised as follows :—

Mr. E. T. Holmes in May reported that " fluosilicate bait (30 lb. sawdust, 12 oz. Na_2SiF_6) was effective, but slower in its action than the ordinary arsenical bait, two days being required to destroy the band utilised for the experiment."

Mr. J. K. Mayo in July reported that successful results were obtained with the following baits :—30 lb. guinea-corn chaff, 12 oz. Na_2SiF_6, and 30 lb. mixed chaff from guinea-corn and bulrush millet, 12 oz. Na_2SiF_6. Unfortunately circumstances prevented Mr. Mayo from remaining to assess the experimental results himself, the work being done by an African. On two occasions in June the writer made observations on the results of ordinary arsenical baiting (30 lb. sawdust, 12 oz. sodium arsenite) and in each case found that 100% of a band of fourth instar hoppers died within 24 hours of the application of the bait.

Conclusions from field tests with sodium fluosilicate baits.

(i) Baits consisting of sodium fluosilicate and one of the following bases : sawdust, chopped hay, guinea-corn chaff or a mixture of guinea-corn and bulrush millet chaff, are as effective as the standard arsenical bait in the Zaria Province ; but they are not so rapid in their action.

(ii) Baits consisting of sodium fluosilicate and guinea-corn bran are ineffective in the Bauchi and Bornu Provinces ; when salt is added to this bait it is more efficient than standard arsenical bait in the Bornu Province.

(iii) The addition of salt to sawdust-fluosilicate bait in the Zaria Province made no appreciable difference to the efficacy of the bait.

Laboratory Experiments with Sodium Fluosilicate.

Three experiments were carried out in the laboratory in order to determine the length of the period between the time of feeding on various poisoned baits and death. A number of fifth stage hoppers were collected and starved for 24 hours before the commencement of the first two experiments, 14a and 14b ; the hoppers used in 14c were not previously starved. One hopper was placed in each of a series of pill-boxes containing a spatulaful of bait, and the times of feeding and death were recorded. The results of these experiments are shown in Table V.

It will be seen that under the experimental conditions the lethal action of baits containing both the normal quantity and half the normal quantity of sodium arsenite was markedly more rapid than that of ordinary sodium fluosilicate bait. From the fact that two of the controls died (Expt. 14c) within 62 hours of being placed in the pill-boxes it is probable that the small cubic capacity of the boxes had an adverse effect upon them ; but it seems unlikely this effect would be more marked in hoppers which had fed upon arsenical bait than in those which had eaten fluosilicate bait.

On 26th June, 42 fifth stage hoppers were put into a wire cage, 3,872 cubic inches in capacity, which contained four small heaps of different types of bait, one in each

corner. A record was kept of the number of hoppers feeding on each bait, the observations being continued for 1½ hours, in which time the position of the cage was

TABLE V.

Expt. No.	Bait used	Time of feeding	Time of death	Period between feeding and death
14a.	A. 30 lb. sawdust, 6 oz. sodium arsenite	8·59	11·25	2 hrs. 26 min.
	B. 30 lb sawdust, 12 oz. sodium arsenite	9·00	11·00	2 ,, 0 ,,
	C. 30 lb. sawdust, 12 oz. Na_2SiF_6 ...	10·22	?	Less than 23 hrs.
14b.	A. See above	9·16	15·02	5 hrs. 46 min.
	A.	11·01	15·27	4 ,, 26 ,,
	A.	13·10	18·30	5 ,, 20 ,,
			Average	5 ,, 11 ,,
	B. See above	9·35	16·47	7 hrs. 12 min.
	B.	9·10	11·06	1 hr. 56 ,,
	B.	9·19	15·02	5 hrs. 43 ,,
			Average	4 ,, 57 ,,
	C. See above	9·12	1·50	16 hrs. 38 min.
	C.	9·11	20·09	10 ,, 58 ,,
	C.	9·10	19·33	10 ,, 23 ,,
			Average	12 ,, 40 ,,
14c.	B. See above	10·00	15·49	5 hrs. 49 min.
	B.	9·50	16·11	6 ,, 21 ,,
	B.	9·45	16·02	6 ,, 17 ,,
			Average	6 ,, 9 ,,
	C. See above*	7·01	14·52	7 hrs. 51 min.
	C.	15·10	17·59	2 ,, 49 min.
	C.	10·37	21·02	10 ,, 25 ,,
			Average	7 ,, 2 ,,
	Sawdust only	Did not feed	11·10 (27th)	Lived 49 hrs. 30 min.
	,, ,, ...	14·59 (25th)	—	Alive after 62 hrs.
	,, ,, ...	10·23 (25th)	10·35 (26th)	Lived 24 hrs. 55 min.
	,, ,, ...	14·42 (25th)	—	Alive after 62 hrs.

* The experiment was commenced at 9.40 on 25th June, but the hopper did not feed until 7·01 hours on the 26th ; all the remainder fed on the 25th.

altered four times in order to avoid differences in light and temperature from attracting the hoppers to a particular corner of the cage. Fifty-five feedings were recorded and are tabulated below.

TABLE VI.

Type of bait	Number of feedings
28 lb. chopped hay, 12 oz. sodium arsenite	27
30 lb. sawdust, 12 oz. sodium arsenite	6
30 lb. sawdust, 12 oz. sodium fluosilicate	15
30 lb. sawdust, 12 oz. sodium fluosilicate, 12 oz. common salt	7

The experiment indicated that chopped hay is a more attractive carrier than sawdust, that there is little difference between sawdust baits containing either poison, and that the addition of salt to fluosilicate-sawdust bait does not render it more attractive. It is realised that too much importance should not be placed upon the results of a single experiment and that the experimental conditions were not by any means ideal. Uvarov[14] has given a précis of the methods of experiments with baits adopted by various workers, but these experiments are concerned with grasshoppers, which owing to their solitary habits present considerably less difficulty than do the gregarious larvae of locusts. It is difficult to conceive of a satisfactory method of testing the attractivity of a series of baits for locust hoppers in the field.

Toxicity of Sodium Arsenite and Sodium Fluosilicate to Man and other Animals.

In a consideration of the desirability of replacing sodium arsenite by sodium fluosilicate as a poison for use in a locust campaign, the question of toxicity to man and stock plays a prominent part, for the only objections to the use of arsenical substances on a large scale are, firstly, the potential danger to man and stock and, secondly, the question of cost. Sodium arsenite has proved to be a highly efficient poison for hopper control in Nigeria during the last two years, and as stated in the introduction to this paper, there have been neither fatalities to man nor any considerable loss of stock.

Burt & Dutt[1] have stated that "sodium fluosilicate, though more toxic than arsenicals to locusts, is almost innocuous, except in very large doses, to the larger animals." The writer's experiments have shown that fluosilicate is an efficient poison against the hoppers of *L. m. migratorioides*, but have not produced evidence that this substance possesses a greater toxicity than sodium arsenite for this species; presumably Burt & Dutt's statement refers to *S. gregaria*. No opportunity for estimating the toxicity of fluosilicate to domesticated animals in Nigeria has yet occurred, but workers in other parts of the world have investigated this matter. D'Costa and Balwant Singh[2] sprinkled a bait containing 50 lb. bran, 2 lb. molasses and 1 lb. sodium fluosilicate, over an area of about one acre in extent consisting partly of young grown barley and partly of young grass; an assortment of 14 domesticated animals were grazed daily for nine days on this area and suffered no ill effects. These workers also carried out two other experiments. In the first, five bulls were fed with doses of 5, 10, 15, 20 and 25 grains of sodium fluosilicate respectively, the poison being mixed with bran mash and molasses; none of the animals developed toxic symptoms. In the second experiment, two bulls were drenched with half a drachm (13·67 grains) and half an ounce (218·75 grains) of fluosilicate respectively; the first showed slight and the second severe symptoms of poisoning, but neither animal succumbed, though both gave evidence of the toxicity of the drug in the abomasum and duodenum when they were destroyed three months later.

From experiments in which barseem was dusted with sodium fluosilicate and fed to goats, Rizk Attia[12] has "concluded that a dose of 1·5 grams (23·15 grains) to a growing goat of about 10 kilos in weight is dangerous, if not killing, and that the lethal dose lies somewhere between 0·136 and 0·148 grams per kilo of live goats." This writer also found that food dusted with sodium fluosilicate is repellent to both goats and rabbits.

Marcovitch[9] found that with rabbits the minimum fatal dose of sodium fluosilicate by mouth was 0·12 grams per kg. and of potassium arsenite was 0·014 grams per kg. He states also that "poison baits with sodium fluosilicate were found to be distasteful to chickens."

Kuhn[6] discovered that the minimum lethal dose (M.L.D.) of calcium arsenate was 38 and 50 mg. per kg. of body weight for dogs and rabbits respectively, while the M.L.D. of sodium fluosilicate was 150 mg. for dogs and 138 for rabbits.

Seddon,[13] working in New South Wales, found that a dose of 20 grains of sodium arsenite was fatal to sheep, but a dose of 6·6 grains of that substance did not produce any ill effects. This writer states that " Under different circumstances there appears to be a great variation in the toxicity of sodium arsenite for sheep, and in hot weather in South Africa a dose of 3 grains proved toxic to 40% of the sheep." Seddon also found that when arsenical bait was broadcasted on pasture, even at the rate of 100 lb. an acre, sheep grazed without obtaining a toxic dose.

Reeves[10] quotes the work of Dr. H. C. Gardiner who " proved that horses and cattle can take, without any external evidence of injury or any alteration discernible upon the most careful postmortem examination, from 20 to 30 grains of arsenic daily, month in month out. Sheep, being comparatively small animals, are more easily poisoned, requiring only from 4 to 8 grains daily. The fatal dose for horses and cows is 300 grains."

Rizk Attia[12] found that sodium arsenate was slightly more toxic than sodium fluosilicate to goats and about $3\frac{1}{2}$ times more toxic to rabbits. Unfortunately no comparative study of the toxicity of sodium arsenite and sodium fluosilicate appears to have been undertaken ; it is hoped to carry out experiments on these lines in Nigeria.

The writer is not aware of any investigations having been made into the toxicity of fluosilicate to poultry, but van Zyl[15] has found " that fowls of average weight ($4\frac{1}{2}$ lb.) could easily tolerate as much as 20-25 mg. ($\frac{1}{3}$ grain) dissolved arsenic trioxide (As_2O_3), administered in the form of sodium arsenite, three times a week for several successive weeks."

King,[5] referring to hoppers poisoned with sodium arsenite, states that " from observations made in 1929 it appeared that birds do not readily take hoppers which are sickly as a result of having ingested poison." On the other hand, with regard to locusts poisoned with arsenical spraying, Thomsen, quoted by Lounsbury, states that " the white stork fed by preference on the dead and dying locusts, and when these were present appeared to avoid healthy ones, as if catching the latter were too much trouble " ; and in Nigeria the writer of the present paper has observed birds of several species feeding, without ill effect, upon hoppers poisoned with sodium arsenite. All workers seem to agree that the danger to birds through eating poisoned locusts is negligible, and in South Africa locusts killed with sodium arsenite have been used for feeding poultry and ostriches.[7]

In an Indian report[16] the following statement, referring to sodium fluosilicate, occurs " It is not poisonous to animals in small quantities but must be considered harmful in quantities of a tola (180 grains) or above."

From the data quoted above, there does not appear to be a very considerable difference in the toxicity of sodium fluosilicate and arsenical compounds for farm animals ; and D'Costa and Balwant Singh's experiment in which from 5 to 25 grains of fluosilicate were administered to five bulls cannot be regarded as evidence in favour of the substitution of that poison for sodium arsenite, for Gardiner has shown that a *daily* dose of arsenic equal in weight to the largest of these fluosilicate doses has no ill effect on cattle. A strong point in favour of sodium fluosilicate, however, is its repellent action to various animals,[9, 12] whereas it is a well-known fact that baits containing sodium arsenite are not repellent to livestock ; in fact it seems that the arsenite is definitely attractive. The following statement occurs in a paper edited by Lounsbury[7] :—" The arsenite used is somewhat saline to the taste, and hence sprayed areas are attractive to animals which are in want of salt . . " ; also in Kenya[4] an ox died after licking an arsenite container. Experience in many countries has proved that there is little danger to livestock from arsenical baiting, but that accidents are liable to occur through carelessness, *e.g.*, animals straying into a poison-bait factory. Harrison[4] has estimated that stock poisoning in Kenya, as a result of

a spraying and baiting campaign against *Schistocerca gregaria*, was " equivalent in the worst area to perhaps 0·005% of animals in contact." From a detailed account of the causes of death given by this writer it is evident that a large proportion of the mortalities were the result of carelessness. In a large scale campaign complete immunity from accidents cannot be reasonably expected, and it is for this reason that the repellent action of sodium fluosilicate to mammals and birds is of paramount importance.

During the testing of fluosilicate baits at Zaria, the writer observed that several species of small wild birds fed readily upon moribund hoppers, apparently preferring them to healthy hoppers, which were more difficult to capture ; the birds did not appear to suffer any ill effects from their diet of poisoned hoppers, which, in one case, was taken daily for three consecutive days. Dogs and wild guineafowl were also seen eating hoppers poisoned with fluosilicate. It seems probable that the repellent action of the poison would not operate after the bait had been ingested by locust hoppers ; but there is little danger of poisoning resulting from the ingestion of hoppers killed by the bait method. In January 1931, Mr. C. H. Wright, Senior Agricultural Chemist, determined the arsenic content of 243 adult locusts killed by spraying with a solution of 5 oz. of sodium arsenite in 4 gallons of water, and of 116 hoppers which had died after feeding upon arsenical bait of standard strength, *viz.*, 12 oz. of sodium arsenite to 30 lb. of carrier. The results of these analyses showed that, in order to ingest the minimum lethal dose of arsenic trioxide, *viz.*, two grains, a man would have to eat as many as 500 adult locusts or 1,000 hoppers.

There are naturally more lacunae in the evidence of the relative toxicity of the two poisons to man. Marcovitch[8] states that one of the advantages of sodium fluosilicate over arsenicals is that " it is considered less dangerous to man " and also mentions that " sodium fluosilicate in small quantities is non-poisonous to man." There does not appear to be any definite record of the minimum lethal dose of this poison for man ; Marcovitch[9] from his experiments with rabbits, quoted above, concludes that it would be 7·2 grams as compared with 0·84 of a gram of potassium arsenite. Owing to the great variability of different species of animals in their reaction to various poisons, it would appear to be unwise to place too much reliance on the accuracy of minimum lethal doses for one organism calculated from experiments on a different organism ; but it seems reasonable to assume that sodium fluosilicate is less toxic than sodium arsenite to man, as man is peculiarly susceptible to arsenical poisoning, the minimum lethal dose of arsenic trioxide being only about two grains. The commercial sodium arsenite used in Nigeria contains about 80% arsenic trioxide.

Before concluding this section of the paper it may be of interest to record the replies received to a circular submitted to all residents in the Northern Provinces of Nigeria at the conclusion of the first arsenical baiting campaign of 1931. Information was requested as to any substantiated cases of poisoning amongst men and domestic or wild animals. A summary of the replies to the circular is given in Table VII.

TABLE VII.

Adamawa Province. A man working in a bait factory developed sores on his stomach and breast which yielded to one treatment.

Bauchi Province. A few goats and sheep died when bait making was first commenced owing to an inadequate fence round the factory. Two dogs, several chickens, one or two wild guineafowl and a few lizards died.

Benue Province. A few guineafowl, chickens, rats, reptiles and insects, are reported to have been poisoned.

Ilorin Province. Some goats and poultry died after feeding on a baited area.

Kabba Province. One goat, one baboon, one hyaena and several wild birds. The baboon and hyaena died after feeding on poisoned hoppers.

Niger Province. One horse, six cows, two donkeys, five dogs, one hartebeest, one duiker, one snake, one crow, a few fowls, three weaver-birds and a few small wild birds. The donkeys ate leaves on which an arsenite tin had been placed and the fowls fed on bait.

Plateau Province. Three dogs, one lioness, one hartebeest, one reed-buck, one vulture and some lizards. The hartebeest had eaten poisoned grass which had been scattered too thickly and the lioness had eaten part of the hartebeest after killing it.

Zaria Province. Two slight cases of arsenical poisoning amongst men.

Kano and Sokoto Provinces. No casualties.

There is no record of autoptical examination of any of the dead animals having been made; but even if we regard all the deaths as being due to arsenical poisoning the losses of economic importance are remarkably slight.

Relative Costs of Sodium Arsenite and Sodium Fluosilicate.

Marcovitch[8] states that one of the advantages of sodium fluosilicate over arsenicals in the United States of America is that it is cheaper. The commercial sodium arsenite used in Nigeria cost from £22 10s. to £24 a ton when supplied in one cwt. drums and from £27 15s. to £28 5s. a ton when packed in drums containing from 50 to 54 lb.; the last-mentioned method of packing is preferable for local conditions, as much of the transporting is done by native carriers. Mr. Uvarov, on the writer's behalf, kindly obtained quotations for commercial sodium fluosilicate from several firms; the method of packing was only stated by one firm. From Mr. Uvarov's figures it seems probable that suitably packed fluosilicate can be obtained for about £10* a ton; but the addition of common salt to baits containing fluosilicate appears to be desirable and salt costs about £9 10s. a ton at Ibadan, a town on the railway about 120 miles from Lagos. As fluosilicate bait contains an equal quanity of poison and salt, each identical with the weight of sodium arsenite used in arsenical bait, the transport charges would be doubled; this is an important matter when baiting is being carried out in places remote from railhead, *e.g.*, the Chad area, which is over 400 miles from Jos. Common salt can be purchased at Mongonu, in central Chad, at the rate of £26 12s. a ton, so fluosilicate plus salt would cost about £8 a ton more than arsenite in this locality. In areas near to the Nigerian Railway the position would be reversed, the fluosilicate plus salt being several pounds cheaper than arsenite.

Experimental Work with various Carriers.

The principal carriers which have been used in Nigeria to date are bran and chaff from various cereals, principally guinea-corn (*Sorghum vulgare*), sawdust, horse-dung, sugar-cane waste and chopped green grass. It seems probable that the supply of sawdust in the future may be inadequate, and the quantity of horse-dung and sugar-cane waste available is limited, and there are several objections to the utilisation of chopped green grass.

In view of the possibility of a shortage of carriers in the future, the writer tested chopped hay impregnated with fluosilicate and with arsenite. The results of the experimental work with fluosilicate-hay baits have been described already. These baits gave encouraging results, and one small-scale attractivity test in the laboratory indicated that arsenite-hay bait was more attractive than sawdust baits containing arsenite, fluosilicate, and fluosilicate plus salt respectively. It was found that cut grass could be converted into good hay by sun-drying for 21 hours (on four consecutive days); experiments carried out by Mr. J. Maule showed that, with a chaff-cutter, 62 lb. of chopped hay (in lengths of about one inch) could be produced in one hour, while a man using a cutlass could produce about 10 lb. in the same period. If the hay is chopped into lengths of about two inches, a man can convert about 13 lb. an hour.

An absorption test showed that chopped hay will only absorb about 82% as much water as sawdust, so it was necessary to increase the strength of the arsenical solution;

*Since this paper was written, the cost of sodium fluosilicate has risen to about £34 a ton.

14 lb. of hay chopped into two-inch lengths was placed in 3 gall. of water containing 6 oz. of sodium arsenite in solution. The preparation of the bait was rather laborious on account of the bulkiness of the hay and the difficulty experienced in the mixing process. At 7.10 a.m. on 22nd June the bait was applied at the rate of 48 lb. an acre to a band of fifth stage hoppers (containing a few adults) about ¼ acre in area. Ten hours after the application about half the band was dead, and in another 45 hours the remaining half had died. It should be mentioned that part of the band had passed over the edge of an old baited area on the morning of the 21st and about one per cent. was dead or moribund before the hay bait was applied; it is known that the majority of the hoppers had not fed upon the old dry sawdust bait before the commencement of the experiment. Application presented some difficulty, as the hay tended to adhere in lumps about half a handful in size; in the fluosilicate experiments the hay was drier and was considerably easier to apply correctly. Chopped hay bait, containing either arsenite or fluosilicate is effective, but there are difficulties in its manufacture and application, and its comparatively poor absorptive qualities necessitate an increase in the amount of sodium arsenite used.

It occurred to the writer that it might be possible to utilise paper as a carrier, and although it is realised that the quantity of this substance available in countries such as Nigeria is limited, it was decided to investigate the matter. Old newspapers weighing 5 lb. were torn up into pieces, with a superficial area of about two square inches, which were then placed in a drum containing a solution of 2 oz. of sodium arsenite in two gallons of water. It was found that all the solution was absorbed by the paper; a previous test had shown that the paper would absorb 1½ times as much water as sawdust, so it was possible to reduce the quantity of poison from 3 to 2 oz. to every 2 gallons of water. Small-scale experiments with hoppers in the laboratory showed that the paper bait was worth testing on a large scale in the field; but unfortunately the writer has had only one opportunity of experimentation in the field to date and that under unsatisfactory conditions. Between 6.15 and 6.30 a.m. on 21st July 2 lb. of paper bait was applied to a band of hoppers about 300 square yards in area and a further 2 lb. to another band about 180 square yards in area. The hoppers were lethargic, as the final ecdysis was imminent; within 72 hours of baiting 15% of the first band and 1% of the second band were dead or dying. In a control experiment with a chopped hay-fluosilicate bait only 1% died in the same period, indicating that the conditions were unfavourable for baiting, as the hoppers were not feeding readily—a conclusion which was verified by observation through prism binoculars. It will be seen that the results were not discouraging and it is hoped to carry out further investigations at the first opportunity.

Summary.

(1) For the first time sodium fluosilicate has been tested as a poison against the hoppers of *Locusta migratoria migratorioides*. This poison was found to be as effective as sodium arsenite in baits when used at the same concentration, *viz.*, 2·44%, but was slower in its action. When guinea-corn bran is used as the carrier it is necessary to add salt to the bait as an attractant; the reason for this is not known, fluosilicate baits containing sawdust, chopped hay and chaff from cereal crops respectively were effective without salt being added.

(2) From an examination of the results of experimental work on the relative toxicities of sodium fluosilicate and arsenical compounds to domesticated animals in various parts of the world, it is concluded that the former is less toxic to stock, but that the increased degree of safety acquired through the use of sodium fluosilicate is not so great as is popularly supposed. A definite advantage of baits containing fluosilicate is that they are repellent to many animals, whereas baits containing sodium arsenite are attractive to stock.

(3) Although sodium fluosilicate is considerably cheaper than sodium arsenite, the addition of salt to baits containing the former—which seems to be desirable—largely vitiates this economic advantage in Nigeria and probably in many other countries.

(4) Chopped hay was found to be a satisfactory carrier when used with either fluosilicate or arsenite ; and a test of paper as a carrier gave an indication that this substance may prove to be a useful accessory carrier for the manufacture of poisoned baits.

In conclusion, it may be said that five tons of sodium fluosilicate are being obtained and that arrangements have been made for a large scale test of this poison during the 1932 hopper campaign ; it is hoped that this investigation will throw further light on the question of the necessity for the addition of common salt to fluosilicate baits.

Acknowledgments.

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PUPAL PARASITISM IN *GLOSSINA MORSITANS* AND *G. TACHINOIDES* AT GADAU, NORTHERN NIGERIA.

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Introduction.

Although theoretical objections to applying biological control methods to *Glossina* exist, it may be doubted whether the possibilities of these methods as a means of attaining at least a local degree of control of tsetse have been sufficiently explored. So far as the writer is aware, the only experiment yet carried out along these lines is that described by Lamborn (1925) in Nyasaland, where an attempt was made to control *G. morsitans* by the artificial multiplication and release of a naturally occurring pupal parasite, *Syntomosphyrum glossinae*, Waterst. The results appear to have been inconclusive. Lloyd, Lamborn, and others have bred out and recorded many Hymenopterous and Dipterous parasites from *Glossina* puparia, chiefly from *G. morsitans* in East Africa, and a full list of species is given by Hegh (1929). Chorley (1929) describing work in Southern Rhodesia was able to show an extraordinarily high rate of parasitism in *G. morsitans*, chiefly by *Mutilla glossinae* and one or more species of a Bombyliid genus, *Thyridanthrax*. It would seem that in the part of Southern Rhodesia where the observations were made, a high degree of control of the tsetse by its pupal parasites must be exerted.

Hitherto there have been few records of parasites of *Glossina* from West Africa. Simpson (1918) working in the Northern Territories of the Gold Coast recorded the following species: *Chalcis amenocles*, Walk., *Dirhinus inflexus*, Waterst., and *Coelalysia glossinophaga*, Turn., from *G. morsitans*; and *Chalcis amenocles* from *G. tachinoides*. These three species of parasites were bred from collections of wild puparia, but little indication is given of the rate of parasitism. In the case of *C. amenocles* in *G. tachinoides* it is stated that " a small proportion " of a large number of puparia was parasitised. Lloyd and Johnson working in Northern Nigeria from 1921 onwards made large collections of puparia, chiefly *G. tachinoides*, but no special notes were kept of parasites or parasitism rates. Austen & Hegh (1922) refer to the occurrence of *Thyridanthrax abruptus* in Northern Nigeria but give no details. In April 1928 Dr. V. B. Wigglesworth during a visit to Northern Nigeria collected puparia of *G. tachinoides* and *G. morsitans* in the Sherifuri area, and from these obtained specimens of a new species of *Thyridanthrax* subsequently described by Austen (1929) under the name of *T. argentifrons*.

The work described below was planned to remedy in some measure deficiencies in our knowledge of parasitism of *Glossina* in West Africa and thus prepare the way for future experiments in biological control should such appear desirable.

Methods.

Large numbers of wild puparia of both *G. tachinoides* and *G. morsitans* are collected in the Sherifuri-Gadau area in order to provide supplies of " clean " tsetse for trypanosome transmission work in the Tsetse Investigation Laboratory, Gadau. These pupae are divided into monthly batches and stored in the laboratory, notes being kept of the emergence rates of tsetse and parasites and of the species of parasites emerging.

A trained staff of pupa searchers is maintained, and as the chart shows, it has been found possible to estimate on their work the seasonal variations in the tsetse breeding rate, the unit employed being the number of apparently viable puparia collected by one man in one day. Empty pupal cases are disregarded, since it was found in the first season that the men tended to confine their attentions to old breeding grounds where immense numbers of empty pupal cases were readily obtained. In the season 1929–30 the men employed were new to the work and obtained far fewer puparia than in the succeeding season. From the figures obtained thus far in the 1931–32 breeding season it would seem that the 1930–31 figures can be taken as a reasonable standard.

For identifications of parasites I am indebted to the Imperial Institute of Entomology.

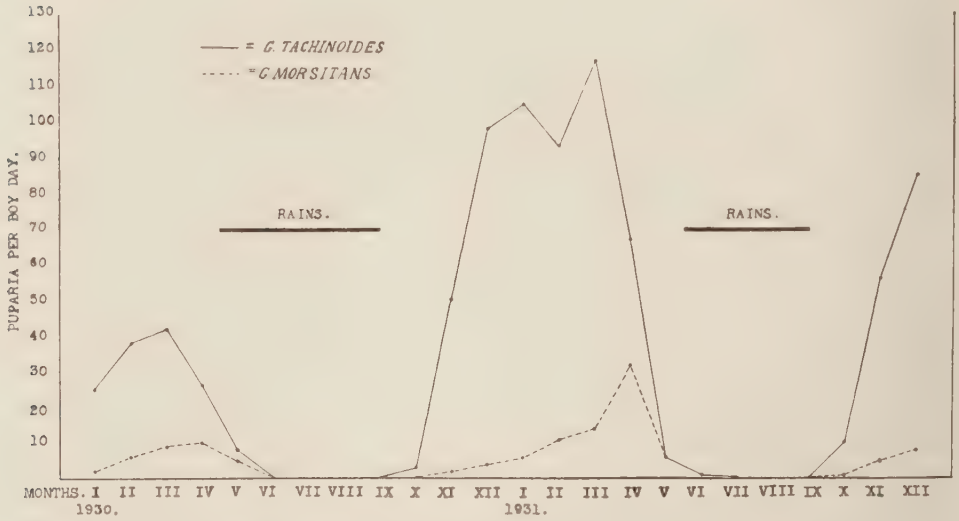


Fig. 1. Chart showing seasonal breeding of *G. tachinoides* and *G. morsitans* based on collections of wild puparia in the Gadau-Sherifuri area, 1930–1931.

Breeding Season of Glossina.

The results of the present investigation confirm the opinion of Lloyd & Johnson (1923–24–27) that the breeding of *G. morsitans* and *G. tachinoides* in Northern Nigeria is largely confined to the dry season. Reference to the chart will show that in the case of *G. tachinoides* breeding reaches its maximum in March, the mid dry season, while the maximum for *G. morsitans* occurs a month later. Rapid falling off in the breeding rates of both species follows. In the wet season after June it is impossible to obtain more than an occasional puparium or a few empty cases. The long grass, heavy rains and saturated soil make search for pupae during the wet season of mid-June to mid-September very difficult, while the fact that both species of tsetse are most dispersed during this season of the year precludes concentration of such pupae as are being produced.

Tables I and II show in general a falling off in the tsetse emergence rates during the hot season months of March-May. This is attributable to the lack of shelter in many of the breeding grounds following leaf-fall and more complete grass-burning, so that the breeding grounds are increasingly exposed to the heat of the sun at a time when this is at its maximum. Chorley (1929) emphasises the importance of this factor in tsetse breeding during the late hot dry season months in S. Rhodesia.

Johnson & Lloyd (1923) have described in detail types of *G. tachinoides* breeding grounds in Northern Nigeria, and nothing need be added to their description. *G. morsitans* puparia are found in association with those of *tachinoides*, though never in the same concentrations. For the purposes of the present work puparia were collected beside long stretches of the rivers Katagum and Kiawa in their course through the Gadau-Sherifuri area.

TABLE I.

The Natural Parasitism Rate in Puparia of G. tachinoides *from the Sherifuri-Gadau Area, 1930–31.*

	Total collections of puparia	Percentage of puparia yielding tsetse	Percentage of puparia yielding parasites	Number of *T. argentifrons* emerged	Number of other parasites emerged	All parasites as percentages of total emergences	*T. argentifrons* as percentage of total emergences
1930							
Jan.	3,977	60·8	0·1	5	—	0·2	0·2
Feb.	5,414	46·4	0·1	4	—	0·2	0·2
Mar.	6,540	55·2	0·05	3	1	0·1	0·1
Apr.	4,007	17·4	0·4	14	1	2·1	2·0
May	1,267	10·8	0·2	2	—	1·4	1·4
Oct.	485	12·0	—	—	—	—	—
Nov.	7,521	37·3	*	—	1	*	—
Dec.	15,878	48·5	*	5	—	0·1	0·1
1931							
Jan.	16,936	47·3	0·2	36	—	0·45	0·45
Feb.	13,346	54·8	0·5	64	1	0·9	0·9
Mar.	18,267	36·7	2·3	427	—	6·0	6·0
Apr.	10,429	30·3	1·2	126	2	3·9	3·9
May	1,846	24·9	0·4	8	—	1·7	1·7
June	134	72·4	—	—	—	—	—

* Less than 0·05 per cent.

TABLE II.

The Natural Parasitism Rate in Puparia of G. morsitans *from the Sherifuri-Gadau Area, 1930–31.*

	Total collections of puparia	Percentage of puparia yielding tsetse	Percentage of puparia yielding parasites	Number of *T. argentifrons* emerged	Number of other parasites emerged	All parasites as percentages of total emergences	*T. argentifrons* as percentage of total emergences
1930							
Jan.	304	44·1	—	—	—	—	—
Feb.	817	48·7	—	—	—	—	—
Mar.	1,346	54·6	—	—	—	—	—
Apr.	1,506	30·7	—	—	—	—	—
May	886	11·9	0·2	2	—	1·9	1·9
Oct.	14	—	—	—	—	—	—
Nov.	251	33·9	—	—	—	—	—
Dec.	672	39·1	—	—	—	—	—
1931							
Jan.	936	39·2	—	—	—	—	—
Feb.	1,530	44·7	0·3	1	3	0·6	0·1
Mar.	2,172	35·7	0·5	11	—	1·4	1·4
Apr.	5,019	20·9	0·5	21	2	2·1	2·0
May	1,806	54·6	0·7	12	—	1·2	1·2
June	87	57·5	—	—	—	—	—

Parasites of Glossina.

Tables I and II summarise the results obtained from the breeding of tsetse and parasites from wild puparia of *G. tachinoides* and *G. morsitans*. During the two years' work, 106,047 puparia of *G. tachinoides* and 17,346 puparia of *G. morsitans* have been collected in this area. From these, three species of parasites have been bred: *Thyridanthrax argentifrons*, Aust., and *Stomatoceras micans*, Waterst., have been obtained from both *morsitans* and *tachinoides*, and a single specimen of *Perilampus violaceus*, F., has been bred from *morsitans*. As the figures show, *T. argentifrons* is by far the most frequently occurring species, and parasitises *G. tachinoides* to a somewhat greater extent than *G. morsitans*. The other two Hymenopterous parasites occur very infrequently and can be of little or no practical importance.

The parasitism rate in both species is lowest at the commencement of the tsetse breeding season in October-November after the rains; it commences to rise in the mid dry season and reaches its maximum in the late dry season in March–April. In *G. tachinoides* the highest parasitism rate recorded for any one month was in March 1931 when 427 specimens of *T. argentifrons* emerged, forming 6 per cent. of the total emergences (tsetse+parasites). In the case of *G. morsitans* the highest rate was in April 1931 when 21 *T. argentifrons* and 2 *S. micans* formed 2 per cent. of the total emergences for that month. Compared with Chorley's figures from S. Rhodesia these rates are very low, and parasites are obviously of much less significance here as controlling agents of *Glossina* than in that country. This may be one reason why there is not a marked drop in the density of either *G. tachinoides* or *G. morsitans* corresponding to that in *G. morsitans* in S. Rhodesia in the late dry season.

It is rather remarkable that not one of the parasites recorded by Simpson from *G. morsitans* and *G. tachinoides* in the Northern Territories, Gold Coast, has been bred in Northern Nigeria from puparia of the same species of tsetses. The two places are on about the same latitude and should have similar climates. It is possible that the distribution of parasites of the genus *Glossina* is more limited than has been hitherto realised. During January 1931, in the course of a visit to Ibi on the River Benue, some 400 miles south of Gadau, 7,549 puparia of *G. tachinoides* were collected. From these no parasites whatever were obtained. This is the only other locality from which large collections of puparia have been made.

T. argentifrons was the only parasite obtained in sufficient numbers to make possible attempts at maintaining and breeding in the laboratory. It was found, however, that like all Bombyliid flies, this species was most unadaptable to artificial conditions and could only be kept alive with difficulty for short periods.

The average length of the developmental period of the parasites obtained can only be very roughly estimated. Normally the *Thyridanthrax* had emerged within six weeks of the puparia being collected. There were, however, instances resembling those described by Chorley in which individual larvae of *Thyridanthrax* apparently entered upon a dormant period lasting for several months. Thus, from the collections of *G. tachinoides* puparia made in April 1931, 119 *T. argentifrons* had emerged by the beginning of June; there was then a long gap, and eventually 7 more *T. argentifrons* emerged during October.

So few of the other two species of parasites were obtained that any statement as to the normal developmental cycle is impossible. In two instances, however, *S. micans* emerged from puparia collected six months previously, thus indicating that under certain conditions the developmental period may be prolonged.

Summary.

A summary is given of the results obtained from the collection of large numbers of the puparia of *G. tachinoides* and *G. morsitans* in the Gadau-Sherifuri area and the breeding of tsetse and parasites therefrom. Totals of 106,047 puparia of *G. tachinoides*

and 17,346 of *G. morsitans* have been dealt with during the two breeding seasons of 1930–31. It is concluded that the Bombyliid, *Thyridanthrax argentifrons*, Aust., is in this area the only naturally occurring pupal parasite of *Glossina* of any importance. This fly has formed as much as 6 per cent. of total emergences from *G. tachinoides* puparia in the month of March, and 2 per cent. of total emergences from *G. morsitans* puparia for the month of April.

Additional evidence is adduced to show that the breeding of both *G. tachinoides* and *G. morsitans* is largely confined to the dry season of the year in Northern Nigeria.

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THE BIOLOGY AND ECONOMIC STATUS OF NEW ZEALAND MUSCIDAE AND CALLIPHORIDAE.—PART I. HISTORICAL REVIEW.

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Introduction.

Blow-flies and house-flies (grouped in the Dipterous family Muscidae in the older sense, including Calliphoridae) are outstandingly abundant throughout New Zealand. The influence of these insects upon the health of man and domestic animals is well known. Though this work deals with the Muscidae as a whole under local conditions, its main object is to record investigations upon the blow-flies with special reference to the depredations of their maggots upon New Zealand sheep.

Any factor that is markedly detrimental to the sheep industry of this country must rank at once as one of major economic importance, since here the sheep population numbers 29,792,516 (1931), upon which, together with other agricultural resources the inhabitants comprising some 1½ million people are primarily dependent. Since blow-flies, or maggot-flies as they are sometimes called, result in an annual loss to our sheep industry of some £400,000, these insects, apart from parasitic worms, are our outstanding problem of the moment in sheep-parasitology. It is of interest to note that, if to this amount is added a loss of £350,000 due to worm infestation, together with an annual sum of approximately £100,000 expended in the control of lice and ked, sheep parasites are costing New Zealand about £850,000 per annum; and a great part of this is not altogether unavoidable.

During the writer's researches into the maggot-fly problem in New Zealand it became apparent that, apart from the infestation of sheep and the influencing factors, there was need for a taxonomic and biological treatment of the blow-flies concerned, since existing accounts dealt too briefly with their taxonomy, and with their biology not at all. This monograph places on record information secured during the maggot-fly researches and treats with (i) a general historical review of the New Zealand Muscidae under past and present conditions, (ii) the taxonomy and biology of the species, especially of the blow-flies injuring sheep, and (iii) the sheep maggot-fly problem.

At the present time the family Muscidae is represented in the Dominion both by indigenous and exotic forms comprising several species of blow-flies, green-bottle flies, the common house-fly, and the stable-fly. Since these insects are intimately associated with land vertebrates, in that the larvae of some live in decaying animal matter, or cause myiasis of man and domestic animals, apart from others the adults of which are vectors of certain mammalian diseases, it is of interest to review the occurrence of these flies under the past and present zoological conditions of the Dominion.

From a zoological standpoint there are two periods in the history of New Zealand, (i) the pre-European era prior to Captain Cook's first visit to these islands in 1769, and (ii) the European era from that year to the present time. Although the inauguration of European influence, bringing about those changes in the natural environment which were to influence fundamentally the future economic development of the country, actually dated from the time of Cook's second visit during 1773–1774, when he liberated the original stock of our wild pigs and goats, it was during the earlier voyage that the first extensive records were made of the fauna and flora of the country.

Pre-European Era.

Prior to the coming of the European, New Zealand had been peopled for some centuries by the Maoris and Morioris, whose progenitors had migrated from Polynesia. When the first European first set foot in the Dominion, the land was covered for the most part by forests of an unusual type, and inhabited by animals equally unique. Among the terrestrial animals were numerous insects and spiders, 2 species of frogs, 15 species of lizards, some 200 species of birds, and 2 species of bats; the last, with the exception of the Maori dog and rat, generally believed to have been brought from Polynesia during the Maori migration, were the only mammals peculiar to the country. The Muscid flies were represented only by blow-flies (mostly blue-bottles), of which there are at least five species, while there was none of the green-bottle or house-fly types, and no blood-sucking forms; the absence of the last is in keeping with the total absence of mammalian parasites (except one species of bat-flea), due to the paucity of mammals.

Under pre-European conditions, the native blow-flies, which breed in decaying vegetable as well as animal matter, did not want for suitable breeding pabulum; prior to the coming of the Maori, however, this must have been considerably limited as compared with later conditions naturally associated with the presence of man. In pre-Maori times decaying lizards and birds—and in these times enormous bodies of the now extinct moas (of which five species are recognised in the genus *Dinornis*) no doubt presented favourable locations for the maggots—were most likely the regular breeding grounds; in this respect it is of interest to note that Hamilton (1893), discussing avian remains from Southland, refers to finding the "pupa-cases of flesh-flies" in the cranium of the extinct New Zealand eagle (*Harpogornis assimilis*). At irregular intervals a localised abundance of decaying vegetable and animal matter was available in the accumulations of kelp (in which at least two native species will breed—Miller, 1909) piled along the sea-shore after storms, or in the bodies of marine fish, whales, dolphins and seals similarly stranded on the coast. Even after storms on the larger inland lakes fresh water fish are, and no doubt were, washed ashore in large quantities; Best (1918) records that the kopupu (*Galaxias fasciatus*) of the Maori is thus found on the shores of Lake Taupo; where such conditions prevailed there was doubtless a local outbreak of blow-flies.

On the advent of the Maoris, a more favourable environment for blow-flies developed as a natural sequence of human occupation. These early immigrants brought with them the Maori dog (now extinct), and Maori rat, and it is possible that the golden-haired blow-fly (*Calliphora stygia*), which occurs in Polynesia as well as Australia, and, as will be shown later, existed in New Zealand during pre-European times, may have reached this country among the provisions of the immigrants. *C. hilli*, another golden-haired blow-fly, recorded from New Zealand and Australia, but not as yet from Polynesia, so closely resembles *C. stygia* that its presence in New Zealand was not noted until 1927 by Malloch. It is possible that both species were in this country prior to European settlement.

Though vegetarian to a great extent, the Maori diet included the flesh of birds, fish, eels, shell-fish, crayfish, and sometimes human beings. There can be no doubt that blow-flies were attracted to animal food where it was killed and being prepared, and that such food became maggot-infested. For example (Matthews, 1910) states that the Maoris carried out shark-fishing on a large scale, and the entrails of these fish were left in heaps which rotted and created a great stench; this practise being indulged in during the warmest period of the year when blow-flies abound.

There is very little information available on maggot-infestation of Maori food in ancient times, and this is probably due to the fact (as stated in a letter to the writer from Dr. Peter Buck) that the Maori could not afford to waste food for such a minor thing, and simply brushed off what he could of the maggots which he considered could do no harm. When eels and fish were spread on stones or hung up to dry, or

where the liver of the shark was hung in order to collect the oil, maggot infestation must have been prevalent, and Dr. Buck tells me that it was the duty of one of the older men, in charge of this drying process, to go round and brush off the maggots. It is unlikely that fresh meat cooked for immediate use would be infested to any extent ; though there is no record on the point, it is possible that blow-flies infested birds and the Maori rat which were stored for future use in receptacles after being cooked and sealed with their own fat. The only definite record of steps being taken to preserve flesh from flies is that given by Skinner (1928), who states that the Chatham Island Morioris (a branch of the Maori people) caught and cured their animal food in the winter during the absence of flies ; thus the flesh of eels and black-fish was cooked, wrapped in flax (*Phormium tenax*), and buried in the ground as a further protection.

Maori corpses on the battle-field must have attracted flies, of which we have some evidence in that on the Kaiangaroa Plains there is a stream called *Wai-iro-hia* or the " river that flows with countless maggots " ; on the banks of this stream a mighty battle had been fought. Again, the Maori custom of keeping a body " lying in state " as long as possible, and in some cases leaving the body exposed to decay in a tree or some other suitable place, certainly caused plagues of flies. These must have been of considerable annoyance, since the Maori used a " fly-flap," very similar to the modern " fly-swat," for the purpose of keeping flies off bodies before burial. Buck (1924) records the manufacture and use of the Maori fly-flap or *patungaro* ; it was made of lightly-scraped flax (*Phormium*) plaited in the form of a square over two crossed sticks, one being longer to form a handle. Another use of the *patungaro* was to protect people of rank from flies, and Buck (*l. c.*) states that the " high chiefs were so *tapu* that dire results took place if a fly that had alighted on their sacred heads subsequently alit on food." In order " to prevent such a calamity attendants were careful to prevent flies from alighting on such chiefs," and the *patungaro* was used for the purpose.

Though the ancient Maori may have been but little concerned with the influence of blow-flies upon his food, that he realised the association of these insects and their maggots with death, is evident from the references to them in Maori lore and legend. Generally flies were referred to by the natives as *rango* or *ngaro*, and maggots as *iroiro* (Best, 1908), while the southern Maori called the blue-bottle *rako* (Beattie, 1919).

To the Maori mind the blow-fly very often figured as a messenger, its droning when in flight being interpreted as a song conveying information to the listener of which the latter was in need; owing to the regular reference to the droning of the fly in such legends, doubtless the large native blue-bottle (*Calliphora quadrimaculata*) was the species concerned. The following legends are worthy of mention.

Wohlers (1874) records the legend of Tama and his wife, Rukutia, who were one day visited by Tutekoropanga and his followers. Rukutia, becoming fascinated with Tutekoropanga, who was much more stylishly dressed than her husband, Tama, eloped with him. Tama, however, after being tattooed, and so rendered extremely handsome, followed, and eventually enticed his wife to return with him. But having secured Rukutia, Tama beheaded her, carried the corpse home and buried it. Tama then " sat day after day in the death-house, and mourned his wife, Rukutia. At last, when the spring season came round and the *tutu* bush (*Coriaria ruscifolia*) put forth new shoots, he heard a humming sound, and then he saw a blue-bottle fly humming, ' u-m-u, notwithstanding my head off, u-m-u.' Upon this Tama got the corpse up again, and opening the box, he found his wife alive. . . "

Another legend (White, 1887) having much the same ending, is that of the brothers Whiro and Hua who had quarrelled over a *totara* tree (*Podocarpus totara*) that Hua had felled and made into a canoe. During the lacing on of the side-boards

of the canoe, Whiro was being assisted by Hua's son, whose finger became caught in the lacing when the latter was drawn tight. Whiro suggested that the boy should put the loop of the lashing over his head, which was done. Then Whiro drew the lashing tight and strangled Hua's son, burying the body beneath the chips from the canoe. Hua fruitlessly searched for his son, and after several days, went and sat near the stern of the canoe. " Soon a blow-fly came and made a buzzing noise over Hua, and then it flew to the hole in the canoe through which the fastening had been pulled which killed his son ; thence it flew to the spot where the body had been buried in the chips, and hovered over it." Hua then recovered the corpse.

Not only blow-flies but also their maggots figure in Maori legend as shown in the story concerning the god Tutakahinahina, who, having died, had been buried in his house. Later on his son " Te Roiroiwhenua heard the voice of his father speaking in his grave : " Here I am buried, look where the earth heaves up." Then Te Roiroiwhenua went to the spot and listened. He heard a gnawing inside the grave ; it was the maggots gnawing at his father. Then he saw two of them crawling out of the grave . . . " (Wohlers, 1874). These legends show that the Maori was well acquainted with the characteristic habits of blow-flies and their larvae.

The following interesting account, sent to the writer by Dr. Buck, illustrates that the blow-fly could be an important actor during the ceremony of disposing of an enemy or punishing a crime. Furthermore, reference here to the " brown-blowfly " points to the fact that the species involved was the golden-haired blow-fly (*Calliphora stygia*, or perhaps *C. hilli*), which thus occurred in New Zealand in pre-European times. " During the ceremony a hole was dug by the officiating *tohunga*, and some object that had been in contact with the victim of the ceremony was deposited therein with appropriate incantations. At this stage a brown-coloured fly, not so large as the blue-bottle, flew into the hole. It represented the spirit of the victim. The priest, with the sod of turf dug from the small hole, crashed down on the fly with the following concluding words of the incantation :—

Tamumu te rango (the blow-fly hums),
Totoro te iro (the maggots crawl).

and if the priest killed the fly, that was the end of the person being dealt with."

European Era.

The scope for blow-fly development in pre-European times was very limited when compared with the conditions that developed under European occupation. As already mentioned, the European influence in the zoological history of New Zealand dates from Captain Cook's visits (1769–1770, and 1773–1774), when he liberated goats, pigs, and sheep in Queen Charlotte Sound. The sheep, however, did not survive, but it is considered that the pigs and goats, which readily established and became wild, stocked the South Island ; indeed, by 1800–1830 the pigs were sufficiently abundant for whalers to secure and carry cargoes of pork from New Zealand to Sydney (Thomson, 1922). Though there are no data to show when rats and mice first reached the Dominion, it is very probable that they escaped from the ships of the earliest visitors. In the years following Cook's visits settlers brought with them the animals and plants of the Old World. Apart from domestic animals introduced by settlers, many game animals (deer, opossum, rabbit, hare, quail and pheasant) were brought in by acclimatisation societies and private individuals. Other animals deliberately introduced were the weasel, hedgehog, and several birds (brown owl, skylark, thrush, blackbird, hedge-sparrow, house-sparrow, yellow-hammer, etc.).

Concerning the present distribution of these exotic animals, the domestic ones, mainly sheep, cattle, and horses, now range over the extensive pastures of the Dominion ; *i.e.*, over practically the whole of the North Island, and the greater part of the South Island excepting the Southern Alps and most of the territory to the west

of these mountains. The more inaccessible areas and the remaining forests are well stocked by game animals, such as deer, wild pigs, goats, opossums, and in places wild cattle and horses. Weasels, rats, mice, and cats occur throughout the country, while rabbits and hares are abundant in places, the former being a serious pest. In all the agricultural and pastoral areas exotic birds abound.

In the establishment of domestic and game animals, the insects infesting them were accidentally introduced; indeed all parasites (excepting certain blow-flies) of domestic animals in New Zealand are exotic species. Among the exotic insects of immediate interest are at least six species of Muscid flies, to which, as well as to the native species, many references have been made in New Zealand literature.

The earliest published record of any of our Muscid flies seems to be that made by Hawkesworth in 1773, when he mentions the "flesh-flies very much like those of Europe;" these were doubtless one of the native blue-bottles, probably *Calliphora quadrimaculata*. The earliest systematic record, however, was by Swederus (1787), when he named this fly as *Musca quadrimaculata*. According to Hutton (1904) the knowledge of New Zealand fauna commenced with the work of naturalists accompanying Cook, the insects being described by Fabricius from 1781 to 1792. But Fabricius records no blow-flies from this country, and it is probable that Swederus named his *quadrimaculata* from specimens secured by Cook's naturalists; there seems to be no other source from which material could have been obtained at that time, which was the period when Fabricius was engaged on the insects brought from New Zealand by Banks, who accompanied Cook.

Some years later Pollack (1838) refers to "the common flesh-fly; and the disagreeable oestrus or gad-fly, whose practice of ejecting its larvae over the smoking viands of the table, render it an intolerable nuisance." The former was no doubt the large native blue-bottle (*C. quadrimaculata*), which frequents the eating places of man more than any other of the native species; the latter was undoubtedly one of the golden-haired blow-flies, *C. stygia* or *C. hilli*, the former of which was first systematically recorded as *Musca laemica* by White in Dieffenbach's "New Zealand" (1843). Hutton (1900) commenting on *C. stygia* states that, though abundant in the North Island for a long time, it had reached Christchurch in 1874, but was there uncommon; up to 1879 he had not seen it in Otago, but records it from Queenstown in 1900. However, Dieffenbach (1843) mentions that the Rev. M. Taylor, of Waimate, had illustrated the life-cycle of this insect, but this was apparently never published; this reference shows that *C. stygia* was undoubtedly sufficiently abundant early in the European era in South Canterbury to be noticed by the settlers.

Shortly after Dieffenbach's visit, the "Erebus" and "Terror" expedition reached New Zealand in 1841, when further collections of insects were made; among these, the only reference to Muscid flies was to *C. stygia* under the original name of *M. laemica* by White (1846).

D'Urville in the "Astrolabe," and La Places in the "La Favorite" visited the Dominion during 1827 and 1831 respectively, and it is probable that from the collections then made Macquart (1843 and 1854) described his four species of Muscid flies—*Calliphora dasyophthalma* (*C. quadrimaculata*), *C. aureopunctata* (*C. hortona*, *C. icela*), *C. auronotata* and *Musca taitensis*.

In the "forties" and earlier, New Zealand residents had commenced to collect and send specimens to England. This material was worked on by Walker (1848), when he described two indigenous species of Muscid flies as *Musca* (*Calliphora*) *hortona*, and *Musca* (*Calliphora*) *icela*, and one exotic species, *Stomoxys calcitrans*, under the synonym of *S. aenos*; the last record is important in that it shows the establishment of *S. calcitrans* in the Dominion at an early date. A little later (1856) Walker described *Musca domestica* from New Zealand under the name of *M. vicaria*, showing that the house-fly also had become early established.

In 1859 the " Novara " expedition collected considerable material in New Zealand and other countries, but insufficient care was taken as to localities, so that some doubt exists as to the accuracy of the records. Schiner (1868) recorded the Diptera from these collections, dealing with Macquart's species *C. dasyophthalma*, *C. aureopunctata*, and *C. auronotata*, and named a new species as *Idia murina* from New Zealand.

Travers (1870) makes some general comments on Muscid flies. He observed a large blow-fly with hairy eyes ovipositing on the surface of a glass bottle taken from a saddle-bag which had been in contact with the sweating side of a horse ; mention of a large fly with " hairy-eyes " identifies this species at once as *C. quadrimaculata*. He states further that not only were rugs " blown," but also it was necessary to hang meat well off the ground ; in this case, however, he gives no indication as to which species of blow-fly was in question, except for his statement that the flies occurred " in dense bush, and high mountains untrodden by man or infested by animals ; " this would tend to point again to *C. quadrimaculata*.

As already stated, the common house-fly (*M. domestica*) was recorded from the Dominion as early as 1856 ; that this insect rapidly became established is shown by some curious references to it. Bathgate (1870) makes the extraordinary statement that the house-fly was responsible for the reduction of native blow-flies, and later (1897) states that it was supposed to have been introduced by means of Australian cattle ships. Regarding the frequent records of the house-fly being a factor in the control of blow-flies, that of Travers (1870) is worthy of quoting. " It has been stated, too, that the numbers of these flies (referring to *C. quadrimaculata*) are found to diminish whenever the common house-fly appears, and a squatter, observing this, and anxious to mitigate the annoyance they caused, once attempted to convey some house-flies from Christchurch to his station on the hills." He failed in his object, however, since " at the end of his first day's journey, having unthinkingly let them out to feed, he was unable to catch them again."

This fantastic idea that the house-fly had a controlling influence upon blow-flies seems to have been generally held during the " seventies," as shown by a statement somewhat similar to that made by Travers, and quoted by Froggatt (1917) from " New Homes for the Old Country " published in 1872. " The most universal creature in New Zealand is the great blow-fly, celebrated for the rapidity with which it can spoil meat. On the most desolate mountain, down on the plains, about stations, in the thick scrub everywhere, we cannot sit at a meal without being visited by one of their tribe. The little civilized house-fly has, however, landed and its refined and gentle presence is rapidly driving into the wilds this noisy spoiler of meat." It is therefore evident that the house-fly was very abundantly established in these early times to have attracted so much fame.

Travers (*l. c.*) further refers to another species of native blue-bottle, smaller than the " common blue-bottle " (*C. quadrimaculata*) which is viviparous and confined to warmer localities ; this species is *C. icela*.

The first systematic attempt to gather these scattered records was made by Hutton (1874), when he listed the insects recorded from New Zealand prior to 1870 ; in this list the following Muscoid flies are given under their original names :—

Musca quadrimaculata, Swederus, Stock. Nya Handl., viii, p. 289 (1787).
Musca laemica, White, Dieff., " New Zealand," ii, 291 (1843) [=*stygia*, F.].
Musca taitensis, Macquart, Dipt. Exot., pt. v, p. 310 (1843).
Musca hortona, Walker, Cat. Dipt. Brit. Mus., p. 894 (1849).
Musca icela, Walker, *l. c.*, p. 897 (1849) [=*hortona*, Walk.].
Calliphora dasyophthalma, Macquart, Dipt. Exot., p. 287 (1843).
Calliphora aureopunctata, Macquart, *l. c.*, p. 130 (1854) [=*hortona*, Walk.].
Calliphora auronotata, Macquart, *l. c.*, p. 135 (1854).
Idia murina, Schiner, Reise der " Novara," Ins. B, Dipt., p. 309 (1868).
Stomoxys aenos, Walker, Cat. Dipt. Brit. Mus., p. 1160 (1849) [=*calcitrans*, L.].

Nowicki (about 1875) recorded *Musca corvina* (*M. autumnalis*), which is the second systematic reference to the house-fly in New Zealand.

Hutton (1881) returned to the subject and re-listed the above species, placing several in other genera, and adding one new species, *Calliphora antennatis*, which, however, is an Anthomyiid; he also included *Calliphora violacea* (Fab.) Macq., as occurring in New Zealand.

Hudson (1889) recorded the European *Calliphora erythrocephala* (Meig.) Desv., under the name of *Musca vomitoria*, Linn., while Meade (1894) identified the *vomitoria* material from New Zealand as *erythrocephala*. Thus *erythrocephala* had reached New Zealand in the early "eighties," if not sooner, and had became well established in both the North and South Islands during the "eighties and nineties." Later (1892) Hudson identified the introduced *Musca domestica*, Linn., and, for the first time, *Lucilia caesar* (Linn.) Desv.,* which Hutton (1900) stated he observed in 1872 at Christchurch.

The most outstanding work on this group of insects was Hutton's "Synopsis of the Diptera Brachycera of New Zealand" (1900), in which he brought the subject up to date. Herein he reduced a number of the species already recorded to synonymic rank, and added one new genus with two new species, *Sepimentum fumosum*, and *S. demissum* (which, however, are Sarcophagids). In this work he discards *Idia murina*, Sch., as not occurring in New Zealand. In the following year (1901) Hutton added two new species, *Calliphora antipodea*, and *C. eudypti*, from the sub-antarctic Islands, and later (1903) a third species, *C. cockaynei* (which Malloch (1924) considers to be a synonym of *C. quadrimaculata*), from the Campbell Islands. In his "Index" (1904), Hutton listed the species recorded by him between the years 1900 and 1901, separating the introduced species from what he considered the indigenous.

Gilruth (1907) recorded the European green-bottle, *Lucilia sericata* (Meig.) Desv., and the writer (1921–22) published the occurrence of the Australian green-bottle, *Chrysomyia rufifacies*, under the generic name *Pycnosoma*. Malloch (1924) and Bezzi (1927) dealt with the New Zealand CALLIPHORINAE, adding no further species, except that Malloch records *Chrysomyia megacephala* (Fabr.); the latter author (1927) makes the first record of the occurrence of *Calliphora hilli* in this Dominion.

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Abbreviations.—A = N. Z. Journal of Agriculture; B = Bulletin of Entomological Research; E = Entomologists' Monthly Magazine; T = Transactions N. Z. Institute; W = Agricultural Gazette, New South Wales.

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*[Miss D. Aubertin states that *L. caesar*, L., does not occur in New Zealand, and it is difficult to say which is the species referred to above.—ED.]

(1922), A., xxiv, pp. 211–12; *Nowicki* (1875), Mem. Krakauer. Akad. Wissen; *Pollack* (1838), "New Zealand," p. 320; *Schiner* (1868), Reise der Fregatte "Novara," Zool. Th. zweit., Band B; *Skinner* (1928), Mem. Bishop Mus., ix, 5, p. 346; *Smith* (1894), E., xxx, pp. 54–57; *Swederus* (1787), Stock. Nya Handl., viii, p. 289; *Thomson* (1922), Naturalisation Animals & Plants N.Z.; *Travers* (1870), T., iii, p. 116; *Walker* (1848), Cat. Dipt. Brit. Mus., & (1854), Suppl.; (1856), Insecta Saundersiana, i; *White, A.* (1846), Voyage "Erebus" & "Terror." Ins. ii; *White, J.* (1887), Ancient History of Maori. ii; *Wohlers* (1874), T., vii, p. 6; (1875), T., viii, pp. 108–23.

THE PHYSICO-CHEMICAL FACTORS OF WATER IN RELATION TO MOSQUITO BREEDING IN TRINIDAD.

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(Plates XL & XLI.)

Contents.

		Page
1.	Introduction	477
2.	Climate and geology of Trinidad	477
3.	*Anopheles tarsimaculatus* in ponds	479
	Description of ponds	479
	Methods and analysis	481
	Summary	486
4.	*Anopheles tarsimaculatus* in rice-fields	486
	Rice-field stations	487
	Analysis	487
	Conclusions	489
	Summary	490
5.	Discussion of results with *Anopheles tarsimaculatus*	491
6.	Experiments with *Aëdes argenteus*	492

1. Introduction.

Some years ago, I made some physico-chemical studies of the factors which perhaps determine the breeding of species of mosquitos in water near London. This work was later extended to Trinidad, British West Indies, which was chosen because it possesses a stable climate, a considerable fauna of species of *Anopheles*, and good roads and laboratory accommodation. The investigation which is here reported was commenced in June 1929 and concluded in April 1931. It was carried out during the tenure of a Wandsworth Scholarship from the London School of Hygiene and Tropical Medicine.

By the courtesy of the Board of Governors, excellent laboratory accommodation was obtained at the Imperial College of Tropical Agriculture in Trinidad. I wish to thank the Principal and Staff of the College, and the Surgeon General and Medical Staff of Trinidad for their kindness to me during my stay in the island.

2. Climate and Geology of Trinidad.

Trinidad lies between 10°03′ and 10°50′ N. Lat., and 60°54′ and 61°56′ W. Long. The northern part of the island is really a continuation of Venezuela, from which it is separated by the Gulf of Paria. Topographically the island may be divided into five zones : (1) the northern range of hills about 5–7 miles in width, with peaks

from 1,500–3,085 ft.; (2) a belt of lowlands extending entirely across the island; (3) a central range with a mean elevation of 500 ft.; (4) a lowland zone south of the central range; and (5) the southern range, which contains the Trinity Hills, the three peaks from which Columbus named the island in 1498.

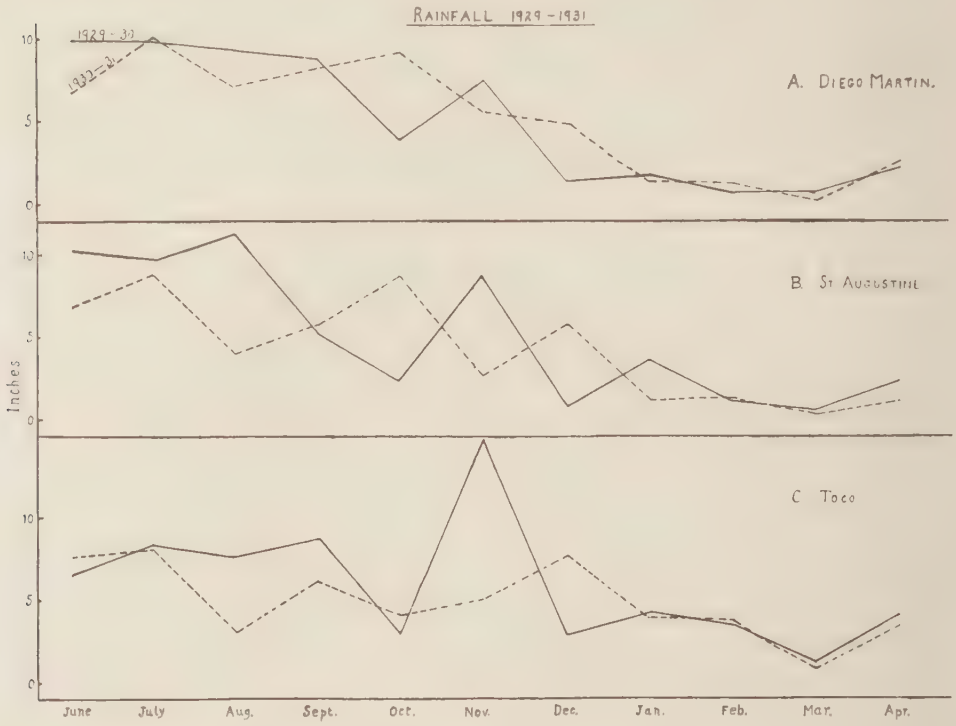


Fig. 1. Rainfall graphs of three stations for the years 1929–30 and 1930–31.

Trinidad lies within the belt of the South-East Trades and normally has a rainy season from the middle of May to the middle of January, the rainfall being less in September and October. The mean annual rainfall varies from 50 ins. in the south-west to perhaps 150 ins. in the northern range. During the year 1930–1931 the rainfall was very low. From June 1930 to January 1931 it showed a curve in inverse proportion to the normal. This is shown in fig. 1. The rainfall curves for three stations in Trinidad are graphed for the years of this investigation. On the other hand the year 1929–1930 had a normal rainfall. There is not much variation in temperature, which seldom falls below 68°F. or rises above 90°F. More than half of the island is now under cultivation. Natural forest still exists in the northern and southern zones.

The northern range consists of metamorphosed sediments. In the central range fine-grained marine deposits, chiefly silts and clays are found; hard rocks, including calcareous beds and siliceous sandstones are also present. The southern range is composed chiefly of deltaic materials, and underlying foraminiferal clays. To the east the higher slopes of this range are formed in the main by sandy and silty beds, marine in character. The plains consist chiefly of swamps and stream deposits; a sandy clay with thin siliceous sandstones. An excellent geological survey of Trinidad has been made by Gerald A. Waring (1926), who gives detailed maps and charts of the geological formation of the different areas of the island.

3. Anopheles tarsimaculatus in Ponds.

At the commencement of this investigation it was noted that *Anopheles tarsimaculatus* was the prevalent Anopheline. This being so, it was decided to confine the investigation to an analysis of the water of the breeding-places of this mosquito, which are very varied in Trinidad (Pls. xl, xli). It occurs indiscriminately in fresh or saline waters, having been found in ground pools, small pools in meadows, the edges of marshes, railway borrow-pits, dirty irrigation canals and rice-fields. It has no apparent preference for light or shade. Six potential breeding-places were selected for analysis. These are numbered 1–6; their position is shown in fig. 2. With the exception of Pond 3, all the ponds were situated in the northern lowland belt; Pond 3 was in the northern range.



Fig. 2. Map showing position of ponds and rice fields.

Description of Ponds.

Pond 1 was a drinking pool for buffalo in the middle of a large savannah about 200 yards from a native village. The pool was open to the sun, about 9ft. by 10ft. in area, and shallow. *A. tarsimaculatus* was found here in large numbers.

Pond 2 was a shallow pool in a rice field drain, about 6ft. by 8ft. in area. It was open to the sun, and about 300 yards distant from a native village. This was a permanent breeding-place of *A. tarsimaculatus*.

Pond 3 was in the course of a small tributary of the Diego Martin River. In size about 9ft. by 11ft., it was well shaded by bamboos along the river banks, and was 200 to 300 yards from the native village. *A. tarsimaculatus* was always found.

Pond 4 was quite near the roadside in the midst of native huts. It was 21ft. by 20ft. in area, and well shaded by surrounding mango trees. This pond was near

a mangrove swamp on the coast; in consequence the water was brackish. *A. tarsimaculatus* was plentiful.

Pond 5 was part of a 2-foot wide irrigation canal of a coconut estate on the coast, with brackish water. It was well shaded by coconut palms. *A. tarsimaculatus* was not numerous, but was always found.

Pond 6 appeared to be an excellent breeding-place. Anopheline larvae were, however, never found in this water. The pit was about 20ft. by 8ft. in area, lying between the railway and a cane-field. It was open to the sun, and about 200 yards from native dwellings.

A few analyses were made of the saline waters of a salt marsh at Chaguaramus (Pond 7) in the north-west of the island and of a pond at Toco (Pond 8) (fig. 2) in the north-east. The results obtained in these two ponds are shown in Tables I and II.

TABLE I.

Results of Analysis of Pond 7.

Ammonia nitrogen (A.N.) in parts per 100,000; chlorides as %; carbon dioxide (CO_2) as ccs. per litre; L=numbers of larvae of *Anopheles tarsimaculatus*.

Month	pH	CO_2	A.N.	Chlorides	L
August 21	7·4	54	0·01	0·5	10
September 22	7·5	76	0·03	0·7	1
October 21	7·4	56	0·01	0·4	3
November 21	7·4	54	0·01	0·3	12
December 27	7·2	48	0·01	0·4	18
January 28	7·4	52	0·01	0·3	10
February 17	7·4	56	0·01	0·1	8
March 23	7·2	62	0·02	0·7	0
April 25	7·2	56	0·02	0·5	0

TABLE II.

Results of Analysis of Pond 8.

Ammonia nitrogen (A.N.) is given as parts per 100,000; chlorides as %; carbon dioxide (CO_2) as ccs. per litre; L=numbers of larvae of *Anopheles tarsimaculatus*.

Date	pH	CO_2	A.N.	Chlorides	L.
1929					
August 10	6·1	72	0·02	2·0	12
September 20	5·8	64	0·01	1·0	10
November 1	6·2	63	0·005	0·3	8
December 13	6·0	58	0·01	0·5	6
1930					
January 8	6·2	64	0·01	0·5	0
March 9	6·0	66	0·005	0·8	0
April 6	6·0	62	0·005	0·6	4
May 24	5·8	72	0·01	0·8	0
July 28	6·2	66	0·01	0·3	4
September 20	6·2	60	0·01	1·0	15
November 23	6·0	62	0·01	0·4	28
1931					
January 8	6·2	58	0·01	0·2	10

Methods and analysis.

The water was collected in 500 cc. bottles. The bottle was immersed in the water, the mouth being about 2 inches below the surface. For the Winkler test for dissolved oxygen the 100 cc. bottles were used. The larvae were collected in a ladle 6 inches in diameter and 3 inches deep. The number of larvae collected by one person in 12 dips was taken as a standard.

The surface temperature, hydrogen ion concentration and dissolved oxygen were estimated in the field. For other tests the water was allowed to stand for 24 hours; the supernatant water without sediment was then decanted off and analysed. In addition to the above, the following chemical factors were determined: ammonia nitrogen, total organic nitrogen, nitrites, nitrates, carbon dioxide gas and phosphates. Chlorides were estimated in certain waters. Nitrites and nitrates were estimated as nitrite nitrogen and nitrate nitrogen. The standard methods of the American Public Health Association were employed, except in the case of phosphates and carbon dioxide. Phosphates were estimated by the Atkins methods; carbon dioxide by the Van Slyke method. I would like to thank Mr. Rodriguez, of the Department of Chemistry of the Imperial College of Tropical Agriculture, for checking estimations of phosphates from time to time. Other estimations were checked at intervals by repetition.

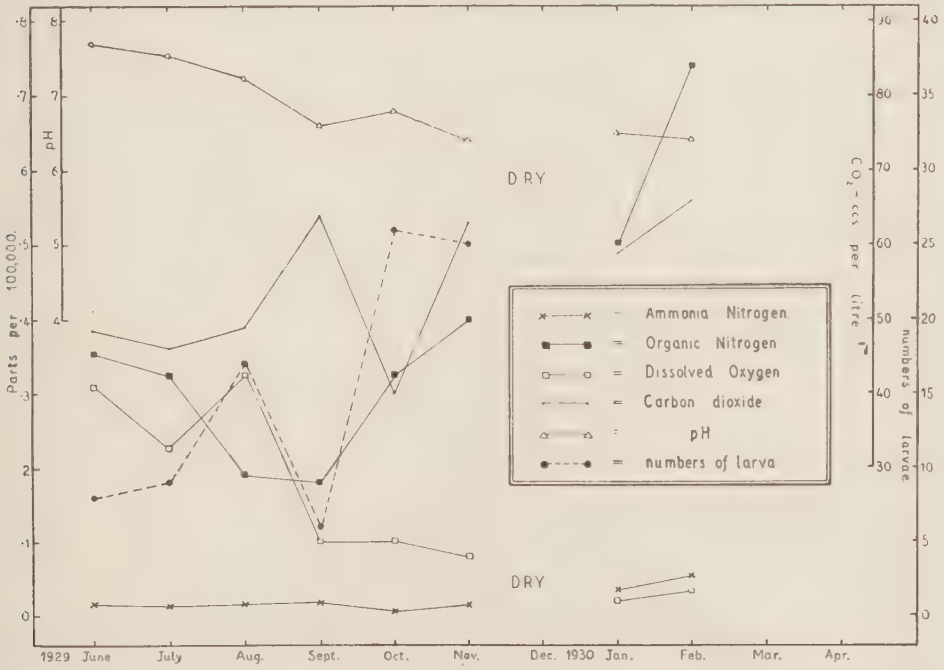


Fig. 3. Results of analysis of pond 1; monthly means.

Carbon dioxide is estimated in cc. per litre and chlorides in Ponds 4, 7 and 8 as percentages. All other factors are estimated in parts per 100,000. The results of the analyses at regular short intervals are too long for publication in detail but some are shown in Tables I, II and III. The results for other ponds and rice-fields are shown graphically: in the graphs I have included all factors which seem at all likely to be important. Nitrites, nitrates, chlorides and phosphorus (as P_2O_5) have been excluded, as they were only present in minute quantities (see below). If the original data on which the graphs were founded are desired, they will be

found filed in typescript in the libraries of the Imperial Institute of Entomology, the British Museum (Nat. Hist.) and the London School of Hygiene and Tropical Medicine.

Temperature.—The surface temperature varied very little. For all ponds it was between 27°C. and 31°C. It was not always possible to take the readings at the same time on different days, so that the readings are not strictly comparable, and have been omitted from the tables.

Hydrogen ion concentration and CO_2 contents.—The carbon dioxide content in most of the ponds varied inversely with pH. Pond 1 (fig. 3) had a pH varying between 6·4 and 7·7; the CO_2 content varied from 35 to 83 cc. per litre, and from fig. 3 it will be seen that there is an inverse variation. The pH of Pond 2 (fig. 4) varied from 5·7 to 7·0; the CO_2 content, varying between 50 and 100 cc. per litre, shows a more definite inverse variation than that of Pond 1. The limits of pH in Pond 3 (fig. 5) were 5·7 and 7·5; the CO_2 content varied between 64 and 103 cc. per litre and also showed variation in inverse proportion. In Pond 4 (fig. 6) the pH varied from 6·4 to 6·8; the CO_2 content varied from 50 to 62 cc. per litre and was in inverse proportion to the pH. The CO_2 content of Pond 5 (fig. 7) was not altogether in inverse proportion to its pH. The variation in pH was from 6·8 to 7·5 and the CO_2 content from 65 to 92 cc. per litre. These five ponds were permanent breeding-places of *Anopheles tarsimaculatus*.

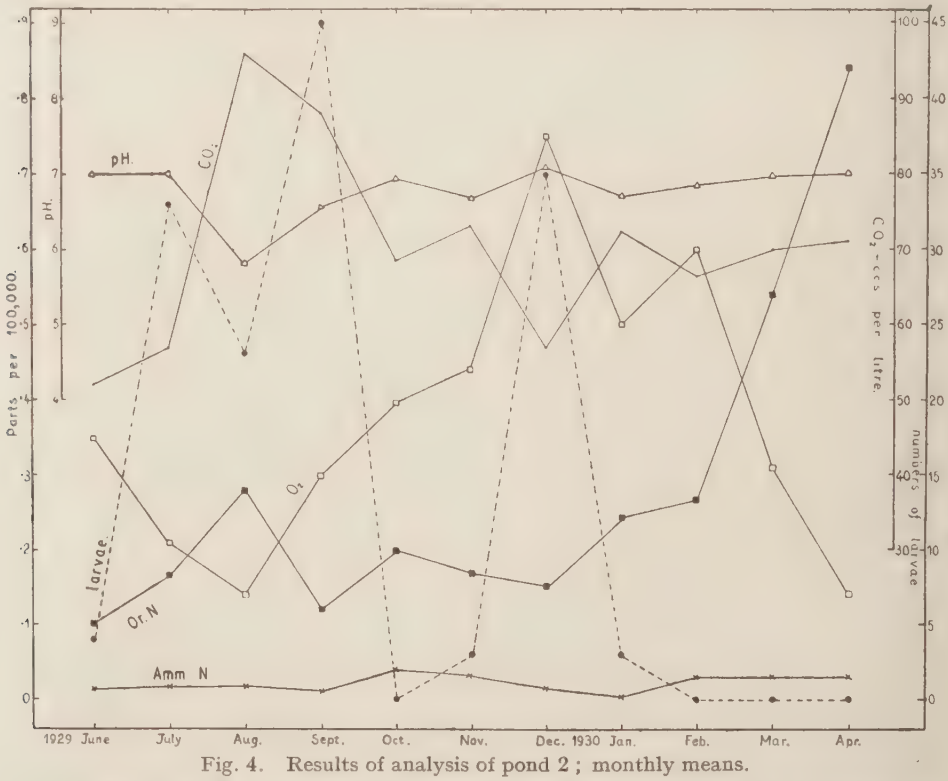


Fig. 4. Results of analysis of pond 2; monthly means.

In Pond 6 (fig. 8), which was not selected as a breeding-place by this mosquito, the pH varied from 6·1 to 7·0 and the CO_2 content from 42 to 60 cc. per litre, showing more or less the same inverse proportion as in the other ponds.

From the tables and figures it is concluded that no definite correlation exists between the reaction of the water and the prevalence of *A. tarsimaculatus*.

Total organic nitrogen and dissolved oxygen.—In most of the ponds the total organic nitrogen content was to some extent inversely proportional to the dissolved oxygen content. In Pond 1 (fig. 3) it was high in June and July 1929, fell in August and September, and rose regularly from October 1929 to February 1930 as the pond dried. The dissolved oxygen content decreased in July, increased in August, decreased again in September, and then fell steadily until February 1929. The total organic nitrogen content in Pond 2 (fig. 4) was low in June, increased in June and July, fell in September, and increased again in October; there was a little decrease in November and December and then a steady rise until April 1930. The dissolved oxygen content fell from June to August, then showed a definite increase until December; it fell in January, rose in February, then fell again in March and April 1930. In Pond 3 (fig. 5) there was a low organic nitrogen content from June

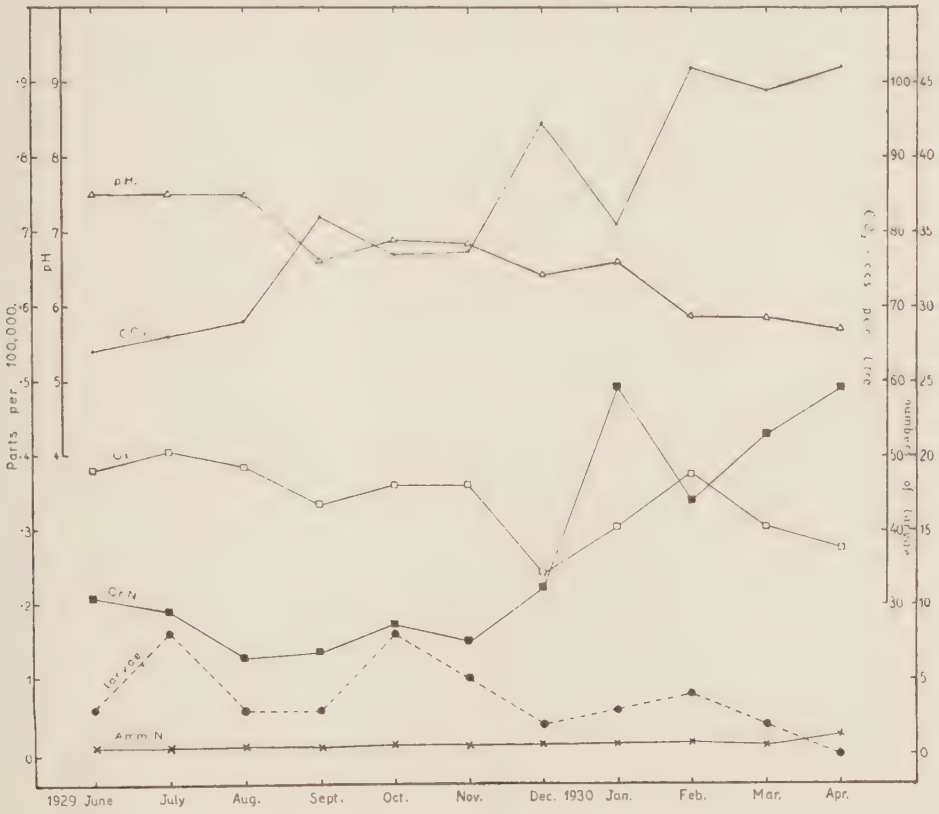


Fig. 5. Results of analysis of pond 3; monthly means.

1929 to December 1929. From January to April 1930 the amount of total organic nitrogen was almost doubled. The dissolved oxygen content was in almost true inverse variation. The total organic nitrogen content of Pond 4 (fig. 6) was low except in August 1929 and January and February 1930. Again in this pond the dissolved oxygen content showed inverse proportion. In Pond 5 (fig. 7) the total organic nitrogen content was never high. On the other hand there was a high dissolved oxygen factor which was not altogether in inverse proportion. The total organic nitrogen content of Pond 6 (fig. 8) was low from June 1929 to January 1930, but showed an increase from February to April 1930. The dissolved oxygen was low in the early months and showed a decrease from February to April 1930. Neither

of these factors, alone or in combination, in any of the ponds had any apparent influence on the prevalence of *A. tarsimaculatus*.

Nitrites and nitrates.—The nitrites and nitrates showed little variation in any of the ponds throughout the year. Figures above 0·01 per 100,000 for either radicle were very rare, and many of the ponds seemed to contain no nitrates or nitrites. There was no evidence of any correlation with Anopheline prevalence.

Phosphates.—Phosphate was not present in large quantity in any of these ponds and had no apparent effect on Anopheline breeding. The highest readings were only 0·02 parts per 100,000 reckoned as P_2O_5. In general the concentrations were a tenth or twentieth of this.

Chlorides.—In Ponds 1, 2, 3, 5, 6, the chlorides were present in very small amounts; the chloride content of Pond 4 was high, running from 0·08 to 0·7 parts per cent., but the increase in salinity did not influence the prevalence of *A. tarsimaculatus*.

Total solids.—No correlation was found between the amount of total solids present in the ponds, and the prevalence of Anophelines.

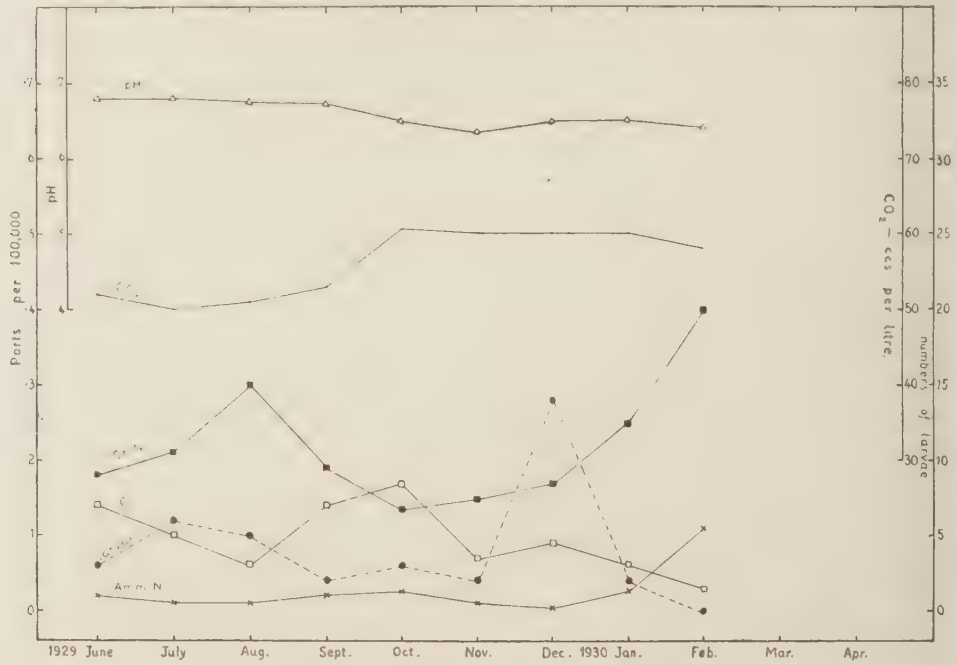


Fig. 6. Results of analysis of pond 4; monthly means.

Ammonia nitrogen.—In Pond 1 (fig. 3) from June to November the ammonia nitrogen figure was fairly constant at 0·01 to 0·02 parts per 100,000. Anopheline larvae were plentiful during these months. In December the pool dried, and after some rain in the beginning of January the ammonia factor was higher, being 0·03 to 0·05 parts per 100,000; no larvae were found during this period. In Pond 2 (fig. 4) the ammonia nitrogen content was low, being from 0·01 to 0·015, from June to September; it rose in October and November to 0·03 to 0·05, fell again in January and was again higher from February to April. Larvae were most prevalent from June to September and in December. The ammonia nitrogen content of Pond 3 (fig. 5) did not vary much throughout the year. Larvae were collected in every month except April. In Pond 4 (fig. 6) from June 1929 to January 1930 the ammonia nitrogen content was between 0·0 and 0·02; in late January and February

the content increased considerably. Larvae were found from June 1929 to January 1930, but none was collected in late January or in February. The ammonia nitrogen content did not vary much in Pond 5 (fig. 7), the limits being 0·01 and 0·03 parts per 100,000. Larvae were not numerous, but were present except in June and December 1929.

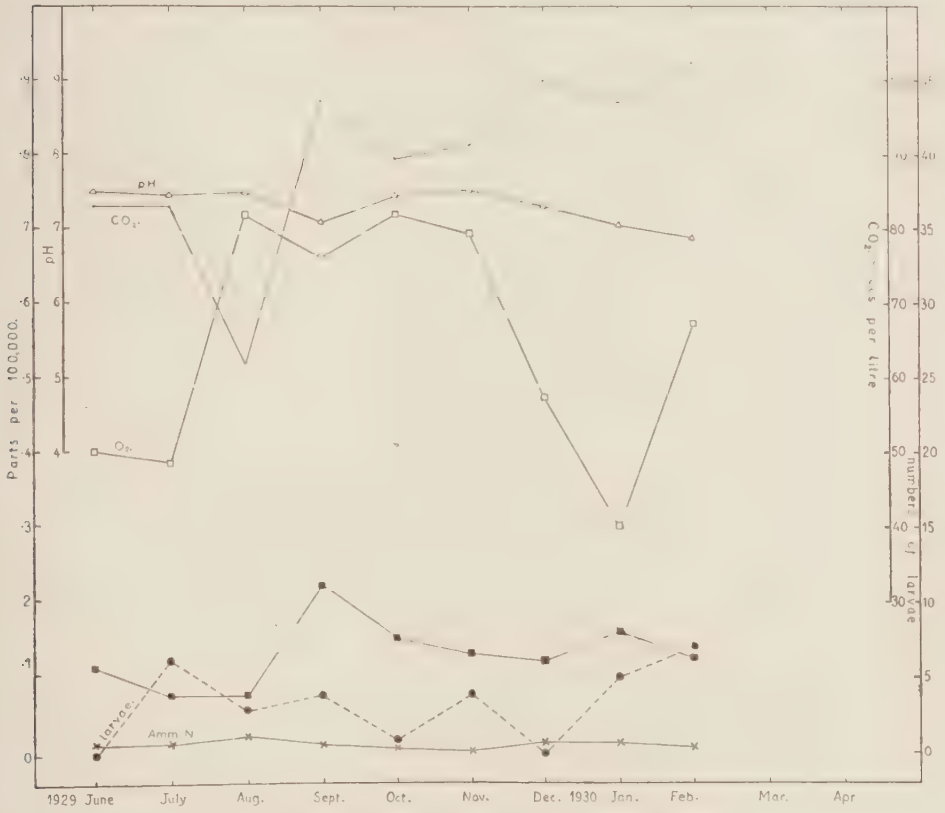


Fig. 7. Results of analysis of pond 5 ; monthly means.

In Pond 6 (fig. 8) the ammonia nitrogen factor was definitely higher than in the other ponds, varying between 0·02 and 0·08 parts per 100,000. No larvae were taken from this pond throughout the year.

From these data ammonia nitrogen appears to have some correlation with Anopheline prevalence. On the other hand, *A. tarsimaculatus* larvae throve well in water in the laboratory with an ammonia nitrogen content of 0·1 to 0·2 parts per 100,000. This suggests that if ammonia nitrogen is really a factor in the selection of breeding-places, it is not the growth of the larvae which is affected, but the oviposition of the female mosquito.

Ponds 7 and 8 were selected on account of their high saline content. Analysis was made also of the following factors : hydrogen ion concentration, carbon dioxide and ammonia nitrogen. Results are shown in Tables I and II. Pond 8 was the more acid, but neither showed much variation in either pH or carbon dioxide content ; the ammonia nitrogen content was low in both ; the chlorides in both varied between 0·1% and 2·0%. Larvae were found when the chlorides were as high as 2·0%.

In the laboratory the larvae of *A. tarsimaculatus* lived for several days in water with chloride content as high as 3·0% and 4·0%; a high saline content of water is therefore not a deterrent to their prevalence.

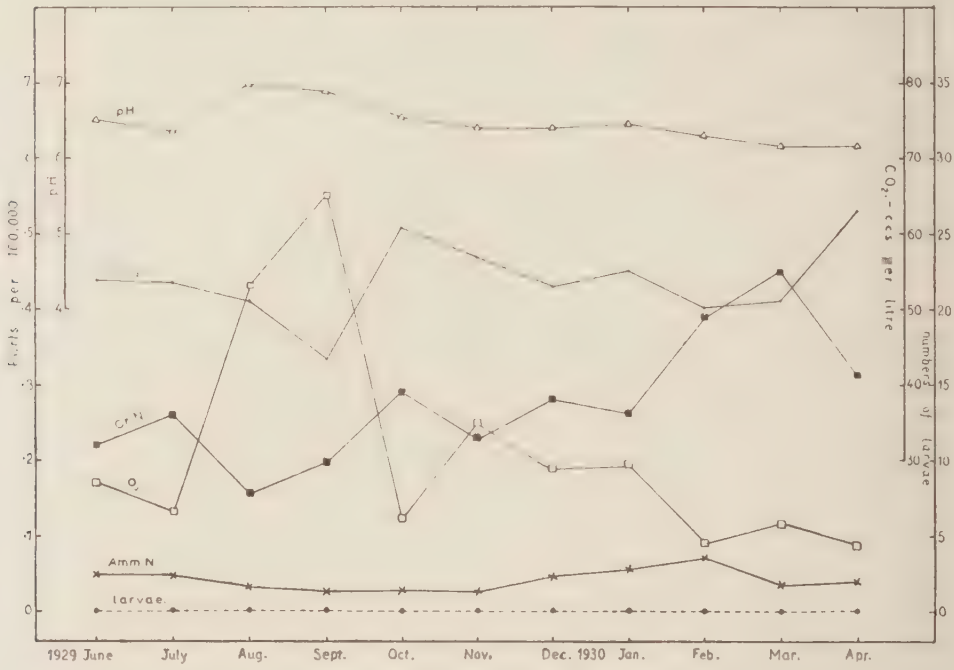


Fig. 8. Results of analysis of pond 6; monthly means.

Summary.

1. An attempt was made to determine whether any correlation existed between the following factors, and the prevalence of *Anopheles tarsimaculatus* in pond waters: hydrogen ion concentration, carbon dioxide, ammonia nitrogen, total organic nitrogen, nitrites, nitrates, phosphates, chlorides and total solids.
2. No regular annual cycle of chemical factors was discovered. Some ponds gave fluctuating, others steady, values for various chemical factors.
3. From the data, ammonia nitrogen is considered to have some effect upon the oviposition of *A. tarsimaculatus* but no effect on larval growth.
4. No definite correlation was found between the other factors and the prevalence of *A. tarsimaculatus*.
5. Chlorides in large amounts were found to be compatible with the breeding of this *Anopheles*.

4. Anopheles tarsimaculatus in Rice-fields.

It appeared from the data collected in the first year of this investigation that ammonia nitrogen was the only factor which showed any correlation with larval incidence. It was decided, therefore, to pay special attention to this factor during a second year's investigation. In the first year the selected breeding-places had been of a general character. As Anopheline prevalence in rice-fields is a problem of great importance in the tropics, rice-field and irrigation-canal waters were selected

for analysis during a second year. Irrigation canals will be referred to as canals for brevity.

Rice is a crop which is said to have a definite effect on the organic content of the soil, resulting in an evolution of nitrogen and marsh gas at certain periods. Harrison & Aiyer found that considerable quantities of nitrogen gas and methane were formed in swamp rice soils. The production of this gas was influenced by two factors—the crop and the organic matter present in the soil. From a general survey made during the first year of this investigation it was found that the incidence of *Anopheles tarsimaculatus* was greater in the canals than in the fields; in the latter, larvae were found when the rice plants were small, but were very rare when the crop was over one foot high. Six rice-field stations were selected and named R1 to R6 (fig. 2). Analysis was commenced in June 1930.

Rice-field Stations.

The six stations were situated in the northern plain (fig. 2) and were in every case open to the sun, all being within a few hundred yards of native dwellings. With the exception of R1, all the stations were the property of East Indians; R1 was the experimental plot of the Imperial College of Tropical Agriculture. Preparation of the fields for crop commenced in June 1930, rice being sown in July; reaping was commenced in November, but owing to the abnormal rainfall some fields were not reaped until December 1930 and January 1931.

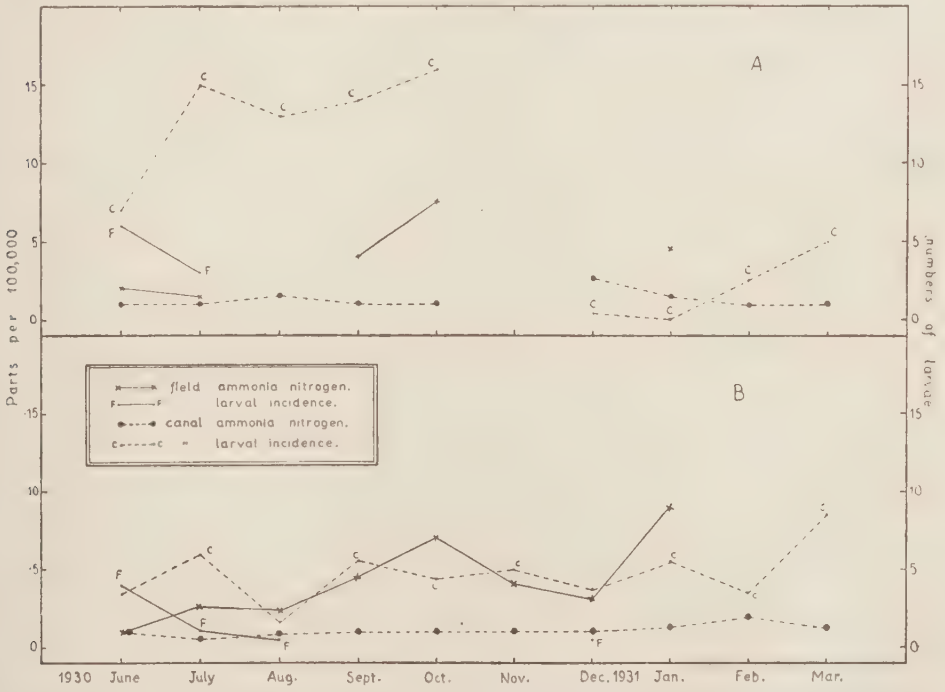


Fig. 9. Relation between monthly means of ammonia nitrogen and larval incidence in field and canal: A, station R1; B, station R2.

Analysis.

Field and laboratory methods were identical with those used the first year. The same chemical factors were estimated, special attention being paid to ammonia nitrogen.

Station R1 (fig. 9A). In the canal the larvae of *A. tarsimaculatus* were present throughout the year; a few were collected from the field in June and July and one in late September 1930. The pH of the canal varied from 6·4 to 7·3, that of the field from 6·4 to 7·0. Nitrites, nitrates and phosphates did not vary much from time to time. The organic nitrogen and carbon dioxide were higher in the field than in the canal; the dissolved oxygen was lower in the canal. None of these factors showed any correlation with larval incidence. Ammonia nitrogen was high in the field in September and November 1930 and in January 1931; no larvae were found during these months. During June and July 1930, the ammonia nitrogen was not much higher in the field than in the canal.

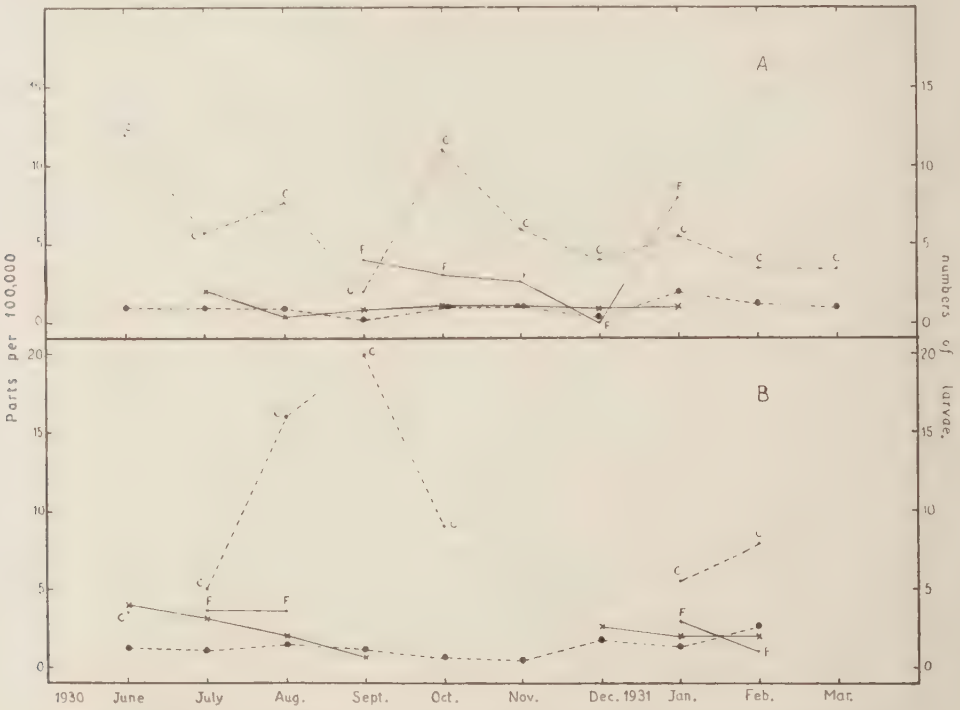


Fig. 10. Relation between monthly means of ammonia nitrogen and larval incidence in field and canal: A, station R3; B, station R4.

Station R2 (fig. 9, B). Larvae were present in the canal throughout the year; in the field they were found in June, July, August and December 1930. The pH of the field and canal did not vary much, the limits being 6·4 and 6·8. Organic nitrogen, dissolved oxygen, carbon dioxide, nitrites, nitrates and phosphates did not vary much. There was no correlation with larval incidence. In the canal the ammonia nitrogen was from 0·0025 to 0·02 parts per 100,000; in the field from 0·01 to 0·10 parts per 100,000, being highest from September 1930 to January 1931.

Station R3 (fig. 10, A). Larvae were always found in the canal and in the field from September 1930 to January 1931. The chemical factors did not vary much; the ammonia nitrogen was not higher in the field than in the canal.

Station R5 (fig. 11, A). Larvae were found in the canal from June 1930 to January 1931, and in March 1931; a few were found in the field in July and September 1930. With the exception of carbon dioxide and ammonia nitrogen the chemical factors did not vary much in the canal or field; the carbon dioxide was

higher in the field. The limits of ammonia nitrogen in the field were 0·01 and 0·12 parts per 100,000; in the drain it was never more than 0·02 parts per 100,000.

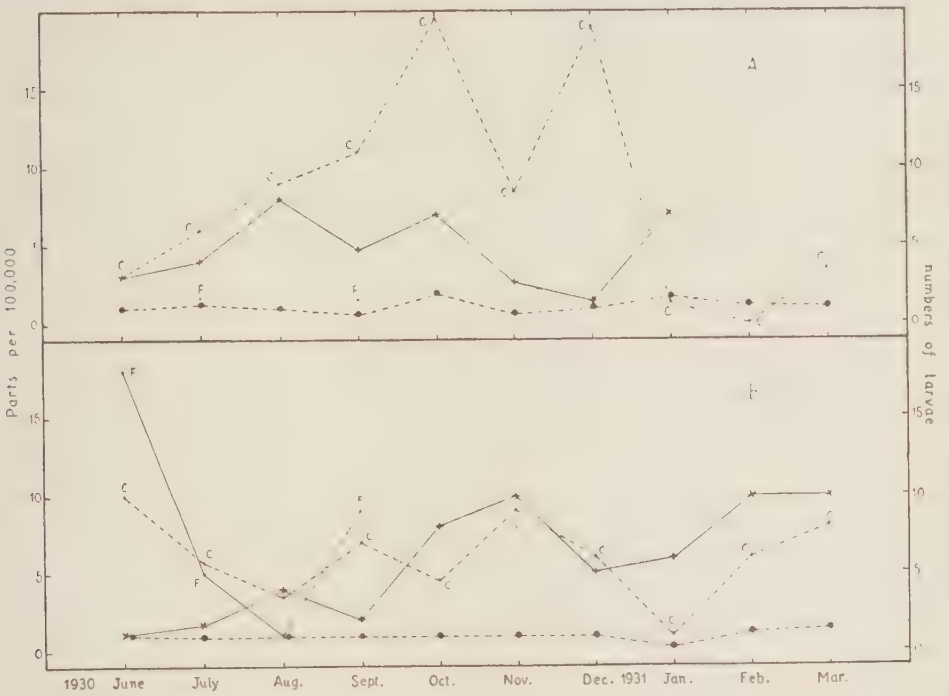


Fig. 11. Relation between monthly means of ammonia nitrogen and larval incidence in in field and canal: A, station R5; B, station R6.

Station R6 (fig. 11, B). Larvae were always found in the canal; in the field they were found from June to September 1930. The chemical factors, with the exception of ammonia nitrogen, did not vary much. The ammonia nitrogen in the field was low in June and July; it rose in August, fell in September, rose again in October and remained high until March 1931.

Station R4 A, B, C and D (fig. 10, B). At Station R4, R4A was the field selected for routine work; in the course of this part of the investigation three adjoining fields were also examined, *viz.* R4 B, R4 C and R4 D. In field R4 D, larvae of *A. tarsimaculatus* were never found. The water of this field has a distinct ammoniacal smell, which may have been due to the presence of some vegetable growth in the water. The pH, organic nitrogen, dissolved oxygen and ammonia nitrogen contents of these fields were estimated. Field R4 D was more alkaline and had a higher ammonia content than the others. It was not possible to ascertain definitely the reason for this increase in ammonia nitrogen. This field may have been more heavily manured or contaminated by sewage in some way.

The contrast between the different parts of R4, from some of which *A. tarsimaculatus* was always absent, is so interesting that the analytical results are given at length (Table III).

Conclusions.

The following factors showed no evidence of correlation with the larval incidence of *Anopheles tarsimaculatus*: pH, carbon dioxide, organic nitrogen, dissolved oxygen, nitrites, nitrates, phosphates. The ammonia nitrogen in the canals lay between

0·005 and 0·03 parts per 100,000, the average content being 0·01 parts per 100,000. In the fields the ammonia nitrogen content rose to 0·12 parts per 100,000, and in field R4 D to 0·18 parts per 100,000. Larvae of *A. tarsimaculatus* were never found in field R4 D. A few were found in the other fields, being more numerous when the ammonia nitrogen content was low. On one occasion only larvae were found when the ammonia nitrogen content was 0·08 parts per 100,000. In the laboratory the larvae of *A. tarsimaculatus* lived for several days in water from field R4 D; out of twelve larvae five pupated and one reached the adult stage. From the data it is concluded that ammonia nitrogen has some bearing upon the prevalence of *A. tarsimaculatus*, affecting the oviposition of the female rather than the life of the larva. But as I only examined the chemical factors I am not in a position to say that the ammonia nitrogen had a direct effect. The possibility that it affects the microflora and, indirectly, the *Anopheles* is not excluded.

TABLE III.

Results of analysis of Station R4—*Fields* A, B, C *and* D.

All factors in parts per 100,000; L=number of *Anopheles tarsimaculatus*.

	A					B				
	pH	A.N.	O.N.	D.O.	L	pH	A.N.	O.N.	D.O.	L
1930										
Aug. 9	5·4	·03	·24	·22	4	6·2	·04	·28	·16	0
,, 22	5·6	·01	·18	·30	3	6·0	·02	·16	·24	3
Sept. 12	5·4	·003	·08	·35	0	5·8	·01	·12	·08	6
,, 30	5·4	·01	·12	·32	0	6·2	·01	·16	·28	9
Dec. 7	5·9	·02	·08	·66	0	6·4	·02	·14	·28	2
,, 28	6·2	·03	·10	·58	0	6·0	·04	·19	·21	0
1931										
Jan. 11	6·1	·01	·08	·60	2	6·0	·03	·12	·26	0
,, 25	5·8	·02	·18	·48	1	6·4	·05	·18	·18	0
	C					D				
1930										
Aug. 9	6·2	·03	·18	·32	0	7·0	·10	·34	·18	0
,, 22	5·8	·04	·28	·22	0	7·2	·12	·36	·10	0
Sept. 12	5·6	·02	·26	·28	4	6·8	·08	·28	·14	0
,, 30	5·8	·05	·18	·38	1	7·0	·08	·26	·22	0
Dec. 7	5·9	·04	·16	·42	2	6·8	·12	·28	·17	0
,, 28	5·6	·04	·20	·34	0	7·2	·10	·23	·18	0
1931										
Jan. 11	5·4	·02	·22	·26	1	7·0	·18	·47	·12	0
,, 25	5·6	·01	·14	·30	6	7·2	·14	·42	·14	0

Summary.

1. An analysis of rice-field and canal waters was made over a period of 1 year.
2. The incidence of *Anopheles tarsimaculatus* in these fields and canals was noted.
3. The chemical factors estimated were pH, carbon dioxide, organic nitrogen, dissolved oxygen, nitrites, nitrates, phosphates and ammonia nitrogen.
4. No correlation was found between the incidence of *A. tarsimaculatus* and the following factors: pH, carbon dioxide, organic nitrogen, dissolved oxygen, nitrites, nitrates and phosphates.

5. In nature the female *A. tarsimaculatus* seemed to prefer waters with a low ammonia nitrogen content, larvae being rarely found in water with a content greater than 0·04 parts per 100,000. In the laboratory the larvae of *A. tarsimaculatus* lived several days in waters with an ammonia nitrogen content as high as 0·12 parts per 100,000. Therefore it was concluded that ammonia nitrogen had some bearing upon the prevalence of this *Anopheles*, affecting the oviposition of the female rather than the growth of the larvae.

5. Discussion of Results with Anopheles tarsimaculatus.

The problem of mosquito selection of breeding-places is now being investigated in several countries. It unfortunately remains complex. There is no doubt that a solution would be of great practical value in dealing with harmful species of mosquitos.

From the data collected in this investigation, the only factor which showed any correlation with larval incidence was ammonia nitrogen. It appeared to affect the oviposition of the female *Anopheles tarsimaculatus*. It must be remembered, however, that in this investigation only chemical factors were considered. Therefore one hesitates to say that ammonia nitrogen has a direct influence on mosquito biology.

Very few natural waters are found which do not contain some trace of ammonium carbonate. This salt may be derived from several sources: it may be produced by the reduction of nitrates by the action of ferruginous sands, or by the contamination of water by the urine of men or animals. Certain low forms of vegetable life also produce ammonia; it is not certain whether they produce it during life or by their death and decay. Thus it may not be ammonia nitrogen *per se* which determines the prevalence of a species of mosquito, but the factor or factors causing the high ammonia nitrogen content. If a pool is contaminated by urine, the female mosquito may avoid it because of an ammoniacal smell which may be perceptible to her. On the other hand, if the high ammoniacal content is caused by decomposition, it may affect the food supply; it is possible that the female will not lay her eggs where there is no nourishment for the larvae. But it seems more probable that the female mosquito is inhibited by a smell than that she has the intelligence to detect a lack of food supply.

In a recent investigation, Rudolfs & Lackey (1929) concluded that the type of decomposition of carbonaceous material was an important factor in the breeding of mosquitos, keeping in mind the fact that certain types of organic acid stimulated the growth of protozoa, which served as food for the larvae, and that certain quantities of humic acid were not detrimental to the breeding of mosquitos. They took some muck and partly decayed vegetable matter from two ponds, one of which was a permanent breeding-place of mosquitos, the other a non-breeding place, and incubated it at 20°C. They found that the quantity of ammonia produced by the decomposing material from the breeding pool remained fairly constant, whereas the amount from the non-breeding pool increased with incubation. There was also an increase in the output of gas from the non-breeding pool, the gas being marsh gas. They concluded that the types of decomposition in the two pools differed. It was found in the laboratory that when gas production was high, organic acids were low, and thus there would be no stimulation of the growth of protozoa, and therefore a decrease of food supply.

It is stated that rice at certain periods produces large quantities of marsh gas from the soil. Unfortunately marsh gas was not estimated in this investigation. The question of Anophelines in rice-fields is being studied in Malaya on a large scale; the results should prove of great value.

Matheson & Hinman (1930) found that species of *Chara* had a marked effect on the development of mosquito larvae. This was not due to a toxic effect but to the mechanical effect of an excessive amount of oxygen given off during photosynthetic activity. The oxygen bubbles were swallowed by the larvae and caused death. In this investigation dissolved oxygen was not found to have any effect on larval incidence.

Boyd (1929) found the temperature, the reaction of the water, carbon dioxide and oxygen in solution, to be important factors in mosquito breeding.

In Russia, Smorodinzew & Adowa (1930) showed that there was some correlation between larval incidence and pH and calcium content; but on studying these factors separately they concluded that calcium alone had no effect.

Kotlyarevskaya (1930) confirmed the assumption that the female *Anopheles maculipennis* did not oviposit in unsuitable breeding-places.

All these workers have attacked this problem by field work; they have tried to find some correlation between a factor or factors and mosquito prevalence in the field, where they were unable to control conditions.

Another legitimate line of attack is to experiment under controlled conditions; similar artificial waters which differ in respect of certain factors can be used to attract the female mosquitos. This can be done in the field as shown by Buxton & Hopkins (1927), or in a cage, as shown by Macfie (1916). These experimental methods are only available for a mosquito which can be easily cultured, such as *Aëdes argenteus*. They cannot, I believe, be used with *Anopheles*.

As part of this investigation, short field and cage experiments were made which showed that the female *Aëdes argenteus* showed a preference for waters with high organic nitrogen content.

Data collected under controlled conditions and concerning one species of mosquito are comparable, whereas the work done in the field by various workers is not so. They have dealt with different species of mosquitos and under different climatic conditions, and their results serve to emphasise the complexity of the problem of mosquito selection of breeding-places. For instance, there is some specific substance in water which prevents mosquitos from breeding, but what inhibits one species of mosquito does not necessarily inhibit another. Thus we have to solve the problem for each species, an immense task. Increasing knowledge strengthens the case for chemical factors as important determinants of mosquito breeding. The accumulation of data may ultimately give us a definite solution of this problem.

6. Experiments with Aëdes argenteus.

These experiments were suggested by the work of Buxton & Hopkins in Samoa. Working with *Aëdes argenteus* and *Aëdes variegatus*, they attempted to discover some of the factors which influenced the female in the selection of breeding-places. They discovered, among other things, that certain organic infusions were more attractive to the female *Aëdes* than distilled water. My own experiments were made in order to find if any correlation existed between the organic nitrogen content of water and the numbers of eggs laid by *Aëdes argenteus*.

Experiment 1.

The first experiment was carried out in a large cage, 3ft. by 3ft. by 3ft., in the laboratory; observations were made over a period of seven weeks. During that time the laboratory temperature was, min. 77°F. to 84°F. and max. 84°F. to 89°F. Six glass pots, 4 ins. high and $2\frac{1}{2}$ ins. in diameter, containing fluids with known amounts of organic nitrogen were placed in a row at one side of the cage about 4 inches apart. Each pot was surrounded by a brown paper jacket to ensure that the illumination was identical; the position of the pots was interchanged daily. A small piece of cork was floated on the surface of each to act as a landing stage for the female mosquito. The pots were half full of the fluid, which was kept at this level by the addition of distilled water.

The fluids were made as follows : *Leaf infusion* : A quantity of dried leaves were placed in enough tap-water to cover it and boiled for half an hour. This infusion was then filtered and sterilised. It was diluted to 1 in 20 with distilled water. Fresh infusions were made at the beginning of each week. The pH and organic nitrogen were estimated at the beginning and end of the week so that each infusion was analysed twice. The average pH and organic nitrogen content of the fluid was then calculated. Grass infusion and watercress infusion were made in the same way. For leaf water a quantity of leaves were placed in enough tap-water to cover them and allowed to stand for 24 hours ; the water was filtered and sterilised as before and diluted to 1 in 10 with distilled water before use. Pond water was collected from a pond near the college and was filtered and sterilised before use. Estimations of all fluids were made as for leaf infusion.

At the beginning of the experiment 100 male and 150 female *Aëdes argenteus*, from a laboratory culture, were placed in the cage. Dead mosquitos were removed when found and replaced from the laboratory culture. The female mosquitos were fed daily on human blood ; raisins and honey were used as food for the males. The eggs laid in each pot were collected daily and counted. The results are given in Table IV as numbers of eggs laid weekly in each pot.

TABLE IV.

Cage Experiment with Aëdes argenteus *showing Numbers of Eggs laid weekly in Pots containing different Organic Nitrogen Contents.*

Week ending	Pot A (Leaf infusion)	Pot B (Grass infusion)	Pot C (Water-cress infusion)	Pot D (Leaf water)	Pot E (Pond water)	Pot F (Distilled water)
Sept. 28	1,735	544	433	613	89	3
Oct. 5	1,295	751	638	349	248	79
,, 12	1,683	539	148	576	322	179
,, 19	1,219	791	387	351	477	331
,, 26	721	763	271	274	443	466
Nov. 2	1,078	970	480	579	294	170
,, 9	578	497	206	285	519	13
Total eggs	*8,309*	*4,855*	*2,563*	*3,027*	*2,392*	*1,241*
Total layings	*42*	*37*	*31*	*36*	*37*	*29*
E.P.L.	*198*	*131*	*83*	*84*	*65*	*43*

The total number of eggs laid was divided by the number of layings in a week, which gave the average number of eggs per laying per pot (E.P.L.—Buxton & Hopkins). The E.P.L. was calculated to the nearest whole number. Total number of eggs and E.P.L. figures are given in Table IV ; from both it seems that Pot A was the most frequently visited, then Pot B ; Pots C and D were equally attractive, and Pot E a little more attractive than Pot F. The pH of the pots did not vary much, being within the limits of 5·5 and 5·0. The organic nitrogen of Pot A was 0·53 parts per 100,000 ; of Pot B, 0·40 parts ; of Pot C, 0·17 parts ; of Pot D, 0·25 parts ; of Pot E, 0·21 parts.

Experiment 2.

This experiment was made in the field over a period of eight weeks. The pots were identical with those used in Experiment 1. They were placed in enamel basins, the bottoms of which were painted with ant poison. Over the pots were placed four-gallon petrol tins with the bottoms removed and a round hole, 3 inches in diameter, cut in the top. All were placed in a garden shelter which was roofed with corrugated iron and covered in on the northern and eastern sides only. The fluid used in the pots was leaf infusion, made as for the first experiment, in different

dilutions. Four pots were put out, Pot Aa contained leaf infusion in a dilution of 1 in 20 ; Pots Bb and Cc contained the same infusion in a dilution of 1 in 50 and 1 in 100 respectively ; Pot Dd contained distilled water. The eggs were collected, and

TABLE V.

Field Experiment with Aëdes argenteus *showing Numbers of Eggs laid weekly in Pots containing different Organic Nitrogen Contents.*

1930 Week ending	Pot Aa (Leaf infusion 1 : 20)	Pot Bb (Leaf infusion 1 : 50)	Pot Cc (Leaf infusion 1 : 100)	Pot Dd (Distilled water)
Jan. 11	51	19	0	13
,, 18	142	70	19	54
,, 25	145	73	21	42
Feb. 1	37	34	17	10
,, 8	111	66	44	27
,, 15	168	106	29	3
,, 22	70	72	14	11
Mar. 1	24	11	1	5
Total eggs	*748*	*451*	*145*	*165*
Total layings	*24*	*22*	*15*	*16*
E.P.L.	*31*	*21*	*10*	*10*

the results, shown in Table V, were calculated as for the first experiment. From the data, Pot Aa was the most attractive, then Pot Bb ; Pot Cc was not apparently more attractive than Pot Dd.

From the results of the two experiments, and taking into consideration errors which might arise from the method of calculation, it was concluded that the female *Aëdes argenteus* preferred to lay her eggs in water containing organic nitrogen in solution, and that the pots containing the highest amounts of organic nitrogen were the most attractive.

APPENDIX.

Mosquitos collected in Trinidad, B.W.I. 1929–1931.

	Locality.
1. ANOPHELINI.	
Anopheles albimanus, Wied. ...	Freeman's Rd., roadside pools.
	Bungalows, Imperial College of Tropical Agriculture.
,, *apicimacula*, Dyar & Knab	Rice-fields, Freeman's Rd.
	River pools, Caura Valley.
	Pools in Cocoa fields, Caroni Rd.
	Roadside pools, Curepe.
,, *argyritarsis*, Rob.-Desv.	River pools, Caura Valley.
	Rice-fields, Freeman's Rd.
	Roadside drain, Cane-field, Curepe.
,, *bellator*, Dyar & Knab	Mora Forest, Valencia.
,, *eiseni*, Coquillett ...	Riverside, Caura Valley.
,, *tarsimaculatus*, Goeldi	Ground pools, Curepe Savannah.
	Rice-fields, Freeman's Rd., Couva, Chaguanas, Caroni, Sangre Grande, Nariva.
	River pools, Caura and Diego Martin Valleys.
	Roadside pools, Moruga, Cedros, Laventille (saline), Toco (saline).
	Caroni Swamp.
	Saline pools, Chaguaramus.

2. MEGARHINI.

Megarhinus trichopygus, Wied. ...	Bromelias in Cocoa field, Caroni.
,, *trinidadensis*, Dyar & Knab	Cut Bamboo, Riverside, Eldorado.
,, *superbus*, Dyar & Knab	Cut Bamboo, Riverside, Caura. Bromelias, Caroni Road.

3. SABETHINI.

Sabethes undosus, Coquillett ...	Cut Bamboo, Maraval and Caura.
,, *cyaneus*, Fab.	Riverside, Caura Valley.
Limatus durhami, Theo. ...	Water in Banana leaves on ground, Maracas Valley.
,, *asullepta*, Theo. ...	Do. do.
Wyeomyia bromeliarum, Dyar & Knab	Bromelias, Caroni, Nariva and Laventille.
,, *quasiluteoventralis*, Theo.	Bromelias, Caura Valley.
Joblotia digitata, Rond.	Cocoa pods, Maracas, Nariva and Caura.
Goeldia frontosa, Theo.	Mora Forest, Valencia.

4. CULICINI.

Psorophora lineata, Dyar & Knab	Pool at root of fallen tree, Cocoa field, Caroni Road.
,, *ferox*, Humboldt ...	Do. do.
,, *cingulata*, Fab. ...	Temporary pools, Freeman's Rd.
Aëdes scapularis, Rond.	St. Augustine.
,, *argenteus*, Poiret	Very common all over the island.
Haemagogus spp.	Mora Forest, Valencia. Guanapo and Caura.
Culex fatigans, Wied.	Maracas Valley, pools in banana leaves.
,, *corniger*, Theo.	Do. do. Caroni Swamp. Roadside pools, Laventille.
,, *coronator*, Dyar & Knab ...	Roadside pools, Laventille.
Deinocerites cancer, Theo. ...	Moruga.
Uranotaenia lowii, Theo. ...	Roadside pools, Laventille.
,, *geometrica*, Theo. ...	Rock pools in River Caura. Roadside pools, Chaguanas, Laventille.

In addition to these there were many unidentified Culicines. These are in the hands of Dr. F. W. Edwards of the British Museum, who has determined the above.

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Explanation of Plate XL.

Fig. 1. Pond 5. Pool in irrigation canal on coconut estate, Cocorite ; breeding-place of *Anopheles tarsimaculatus*.

Fig. 2. Salt water pool on coconut estate, Chaguaramus ; breeding-place of *Anopheles tarsimaculatus*.

Figs. 3 and 4. Irrigation canal of sugar-cane field at Caroni, also used as drinking place for buffalo. *Anopheles tarsimaculatus* breeding freely.

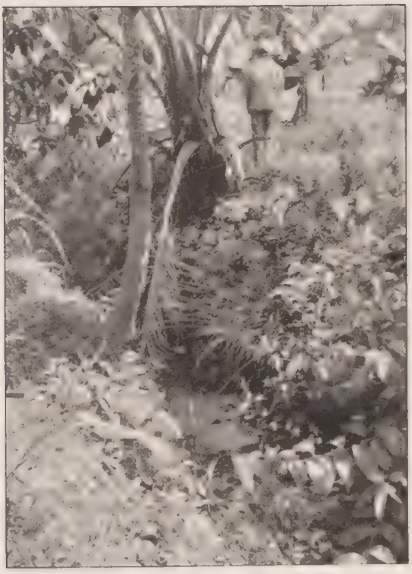


Fig. 1.

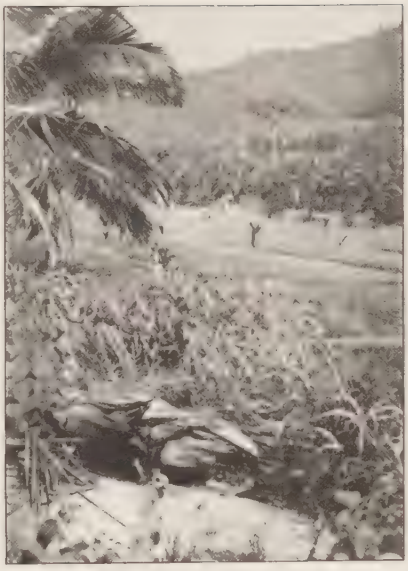


Fig. 2.



Fig. 3.



Fig. 4.

Anopheline Breeding Places in Trinidad.

Explanation of Plate XLI.

Fig. 1. Pool at edge of cane field at Caroni ; breeding-place of *Anopheles tarsimaculatus*.

Fig. 2. Irrigation canal in cane field at Caroni ; *Anopheles tarsimaculatus* breeding freely along the edges of canal, but not found in smaller channels.

Fig. 3. Pool in Mora Forest, Valencia ; breeding-place of *Anopheles tarsimaculatus*.

Fig. 4. River pool well shaded by surrounding trees, Caroni Road ; breeding-place of *Anopheles tarsimaculatus*.



Fig. 1.



Fig. 2.

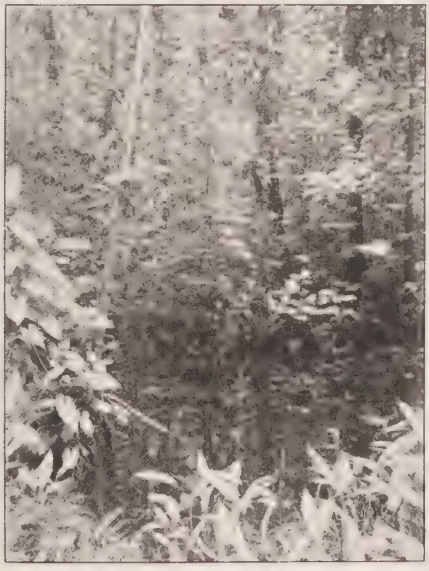


Fig. 3.



Fig. 4.

Anopheline Breeding Places in Trinidad.

THE TSETSE PROBLEM ON THE EASTERN CATTLE ROUTE IN THE GOLD COAST.

By

A. W. J. Pomeroy, M.B.E.

and

K. R. S. Morris, B.Sc., A.R.C.S.

(Plates XLII, XLIII and a Map.)

Introduction.

The purpose of the work described in this paper may be summarised as follows : (*a*) An investigation into the possibilities and economic value of controlling tsetse in certain areas of the Northern Territories of the Gold Coast ; (*b*) the application of control measures ; (*c*) a careful study of the effect of the measures undertaken.

The organisation of definite research on tsetse and trypanosomiasis in the Gold Coast was commenced in December 1925. From previous reports and correspondence it appeared that the veterinary side of the problem was held to be of more importance than the human side, and in consequence research was undertaken on the main cattle route leading from the French Territory of the Haute Volta to Kumasi, in Ashanti.

As there was some doubt as to the true source of infection, a locality was selected for investigation (Yeji on the Volta river) mid-way between the French border and Kumasi, and the cattle passing through were examined for trypanosomiasis. Examinations of blood-films from the cattle were also made at the Border Quarantine Station and at Kumasi, over a thousand animals being examined between November 1926 and March 1927. The result of the work showed that the infection rate at the border was very low, at Yeji there was a marked increase in infection, while at Kumasi, the distributing market for cattle, the infection rate had increased by as much as 60% in the wetter months.

It was evident that a vicious circle of infection from fly to cattle and *vice versa* was taking place all the way down, and funds were provided by the Government to clear a considerable portion of the Cattle Route as an experiment. The result has been to demonstrate a definite control of tsetse in the areas cleared and a consequent reduction in the rate of trypanosome infection in cattle passing down the route.

Later, a project was put forth by the Veterinary Department to establish a cattle breeding centre in the Accra Plains area, in the Colony, and it became necessary to ascertain the prevalence of tsetse there in conjunction with cattle breeding experiments and the control of rinderpest. The results of the investigations will be mentioned separately.

During the course of the investigation on cattle, statistics were obtained with regard to human trypanosomiasis. It appears that sleeping sickness may be of more importance than previously realised, and research is being carried out on the medical side by the pathologist. At the same time an experimental clearing was carried out at Makongo, an endemic centre of the disease, and this will be described in an Appendix.

Trypanosomiasis in Cattle on the Main Eastern Cattle Route.

Blood-smears were taken from the cattle at the border quarantine stations, at Yeji, half-way down the route, and at Kumasi, the main distributing centre. The method employed was the same throughout, thin smears stained with Leishman. Admittedly this method does not give an indication of the entire number of the infections, but as the error was approximately the same throughout, the figures

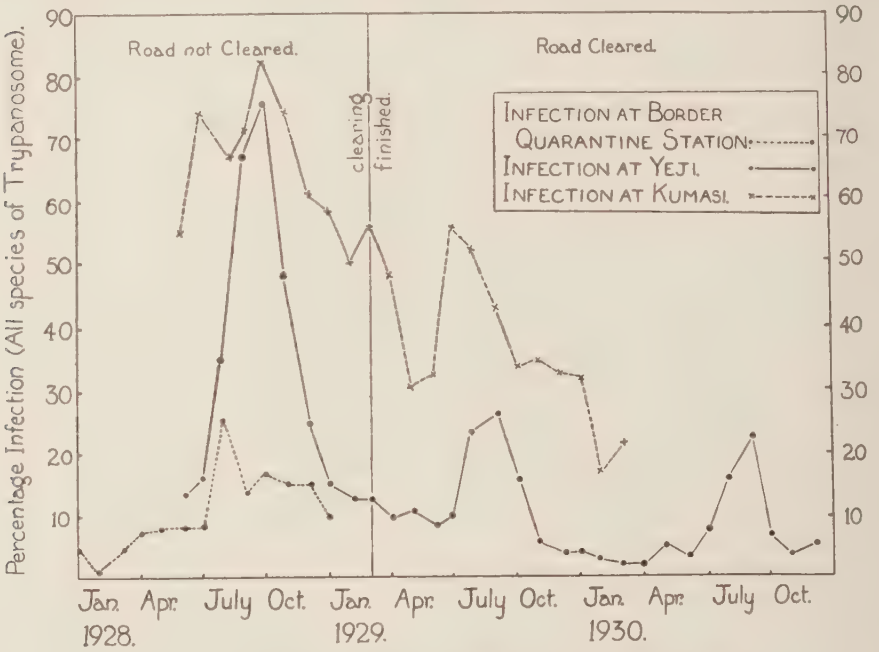


Fig. 1. Trypanosome infection of cattle on the Eastern Route.

still retain their value from a comparative point of view. Diagnosis of the slides was made by the pathologists attached to the Tsetse organisation. *Trypanosoma vivax*, *T. congolense*, *T. brucei*, *T. tragelaphi* and *T. theileri*, were found in the cattle, *T. vivax* predominating. The combined infection rate at each of the three experimental stations is shown on the attached chart (fig. 1). There is a fairly close relation between infection rate and rainfall, an increase in the latter being followed by a rise in infection, owing to the increase and spread of tsetse during the rains. The double peak of infection at Kumasi appears to correspond to the double rainy season, consisting of a short period of heavy rain in June and the main rains in August to October, which only occurs from Yeji southwards (fig. 2).

It will be seen from fig. 1 that after clearing the route there was a remarkable fall in the infection rate, and this could hardly be due to anything but the clearing measures carried out. At the same time it is noticeable that the dry season infection rate at Yeji for 1929 and 1930 is lower than the frontier rate for the same season in 1928. This points to the fact that other influences besides our own clearings were operating in 1929 and 1930. There are two reasons which might account for this, the unusually heavy rainfall in the north in 1928, and clearings carried out in French territory.

Each month in 1930 was a little lower than in 1929, which would be due to the increased efficiency of the clearings in the second year and to the breaking of the

vicious circle of infection between cattle, fly and game. At the same time *T. congolense*, which had been present in a very small percentage of the infections before clearing, disappeared entirely in 1929, but reappeared again in 1930.

This apparent anomaly is explained by entomological observations. At the Nasia River, which was by far the densest fly belt, tsetse were by no means excluded from the clearing during the wet season of 1929, whereas in 1930 they were found only in negligible numbers in the clearing. At this spot in 1929 *T. vivax* was the commonest trypanosome found in dissected flies, and it was also found in game animals shot close to the cattle route in that year, but in an equal number of examinations in 1930 no pathogenic trypanosomes could be found, showing that the cattle-fly-game circle of infection was now broken.

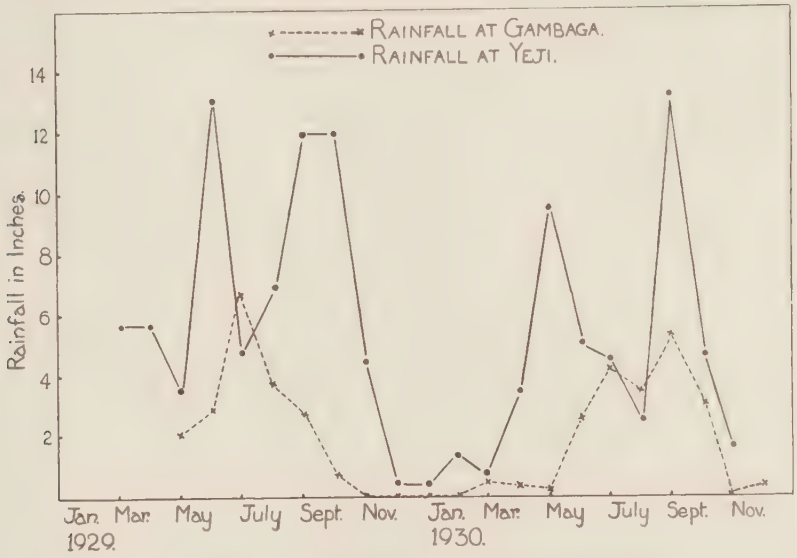


Fig. 2. Rainfall on the Eastern Cattle Route, 1929–1930.

At the Tamne River tsetse were entirely excluded in the first year of clearing, but in 1930 they were found entering the clearing again in some numbers. An examination of local non-humped cattle from this neighbourhood has shown the presence of *T. congolense* but not *T. vivax*. Doubtless it was from this source that the fly got its infection which it transmitted to the passing herds of imported cattle. This small increase in *T. congolense* infection was not sufficient to affect the general fall in infection rate due to the increasing effectiveness of the other clearings.

The results of the pathologist's work have been published in the Reports of the Medical and Sanitary Department, Gold Coast Colony, 1928–1929 and 1929–1930.

General Description of the Country.

In order to present a clear and concise picture of the ecological conditions governing tsetse incidence along the cattle route, a brief general description of the terrain is essential, and each important fly-belt requires to be dealt with in some detail as there is a considerable difference with regard to the habitat of the fly and the distribution of the species.

From the French border to the Nasia River, the farthest point at which clearing was carried out, there are three distinct types of country. From the French border to the Gambaga scarp, a distance of about 35 miles, the cattle route runs through

the heavily populated Kusasi district. The geological formation is of granite, consisting of a series of rolling uplands and fertile well-watered valleys. The local Kusasi people are an agricultural race, never congregating together in towns but living in widely scattered compounds, the whole of the ground being therefore from time to time under cultivation. A considerable number of local non-humped cattle are maintained in this district by the pastoral Fulani. Intense cultivation, grazing and the cutting of bush for firewood, have produced a fine open country of cultural steppe, thick bush only occurring along the larger rivers, the Red and White Voltas with their main tributaries.

At the base of the Gambaga scarp there is a narrow belt of dense thickets, with occasional tall trees, following the course of the Morahgo river. The escarpment, which faces north, is very precipitous, rising from 800 to 1,000 feet in height and is formed of sandstone rock with a scree of boulders and loose soil at the base. The original cattle route up the scarp followed a ravine, the ascent being a matter of considerable difficulty; this route has now been improved.

The country above and south of the scarp is hilly, with frequent outcrops of sandstone through a very thin sandy sub-soil. On the higher slopes the vegetation consists of sparse scrub and small trees, and along the streams there always occurs a fringe of evergreen vegetation. Southward as the terrain gradually falls away from the elevation of the scarp, the streams get larger and the vegetation heavier, a tall woodland with occasional open grassy glades occurring in the valleys, and thick orchard savannah covering the drier ground.

Between the villages of Jowani and Tundi the sandstone formation is replaced by a clay shale, and the character of the country again alters, becoming flat, with many open grass savannahs, especially along the course of the Nasia River. These open grass flats are subjected alternately to flooding and fierce grass burning which prevents tree-growth, but around the edges are found belts of acacia thorn and wild quince, which in turn are replaced by the heavier vegetation of the usual orchard bush.

Distribution and Nature of the Fly-Belts.

The border quarantine station of Mogonori, on the Morbiri River, affords an ideal example of the effect of clearing and farming in driving out tsetse. In 1928 the cattle-crossing and the surrounding country had been cleared of vegetation by the continual grazing of live-stock and the collection of firewood. The station however was closed in 1929, and there was a re-growth of dense wet-weather vegetation consisting of long grass and short creeping thorny scrub (*Mimosa asperata*) which clothed the river bank. This re-growth, together with the few trees remaining, formed just sufficient shelter for *Glossina tachinoides*, which was found in quite large numbers regularly in July and August. This was obviously a secondary fly-belt resulting from migration up the river from its junction with the Volta some six miles distant. The interesting feature of Mogonori is the complete absence of wild game; every possible source of food supply must therefore be considered, and the following list indicates the available food:—

(*a*) Human beings congregated at the actual crossing but did not wander far up or down stream; a small concentration of tsetse was frequently found at this point.

(*b*) Sheep and goats were still coming in by this route and, after swimming the river, invariably rested and grazed over a small area on the south bank.

(*c*) Large quantities of duck, as well as geese and herons, habitually rested on the sandbanks in mid-stream and on the banks during the middle of the day when tsetse are most active, but no evidence had been obtained to date as to whether tsetse ever fed upon them.

(*d*) The other concentration of tsetse was up a small tributary one mile to the west, where crocodiles and monitors (*Varanus* sp.), which were very numerous, appeared to be the only food supply.

(*e*) Amphibia must be included in the possible food list, because not only were they everywhere numerous, but because they have been found to be readily attacked by tsetse in laboratory experiments.

In July and August a number of dissections were made as shown in the following table. It will be observed that in July there was a very high percentage of reptilian blood as compared with mammalian, but in August the reverse condition obtained. It is suggested that this phenomenon may be explained in the following manner. In July the Morbiri River was still at a low level and crocodiles and *Varanus* on the sand-banks were easily accessible to tsetse. The river rose at the beginning of August, the reptiles were dispersed by the flood, and the food of the fly was restricted to human beings and live-stock at the crossing. Generally speaking the fly was in poorer condition than in July, which would appear to be the reason for the decrease in the number of pregnant females. In spite of the high percentage of reptilian blood, it is remarkable that no infection with *Trypanosoma grayi* was found.

TABLE I.

Blood Content and Infection of Glossina tachinoides *at Mogonori.*

Date	No. examined	No. with ingested blood	Percentage mammalian blood	Percentage reptilian blood	Percentage females with larvae	Infection
July 1929	84	19 (22%)	25%	75%	25%	1 *T. vivax* (1·2%)
August 1929	202	59 (29%)	75%	25%	12·5%	Nil

The Tamne is a slow-flowing river, reduced to a chain of pools in the height of the dry season, but subject to much flooding in the rains. Tall vegetation was confined to a very narrow fringe on each bank. The dense growth was not continuous, certain stretches of the river banks being open and covered only with a heavy growth of tall elephant grass during the rainy season. After the annual grass-fires the country is bare and the shade reduced to a minimum. Smaller antelopes are present in the low-lying ground and herds of local cattle and sheep from the neighbourhood are watered here in the dry season. Crocodiles and monitors are extremely common at the river itself. Before clearing, *Glossina tachinoides* was very abundant but no *G. palpalis* were found. Further observations gave evidence that there is a marked seasonal distribution of *G. tachinoides* here. From the beginning of February to the end of June there is a decided general increase in tsetses. With the advent of flooding there appears to be a dispersal of the fly, since in September when flooding was extensive it was almost impossible to find tsetse after most careful search, a total of only six flies being caught in ten days. This low tsetse incidence continues until the middle of the following dry season ; in January 1931 only four tsetse were found in two days search. An observation made on 10th February 1928 showed an abundance of tsetse, no less than thirty being taken in one morning. It appears therefore that there must be a very marked increase of tsetse at this time of the year.

No further fly-belts are encountered until the Morahgo River is reached, the small streams crossing the route being free. The very open nature of the country seems to be the factor responsible for this condition.

There is a narrow belt of uninhabited country extending east and west below the scarp, through which runs the Morahgo River, the actual banks of the river being covered with only sparse vegetation owing to the rocky nature of the soil. The stream bed itself is composed of sand washed down from the scarp with occasional exposures of rock. Close to the water's edge is a continuous fringe of short grass and small bushes, conspicuous among which is *Mimosa asperata*. The alluvial soil of the river valley maintains a growth of tall woodland, dense thickets and occasional glades of rich grass land. Game abounds in this area, including buffalo, water-buck, hartebeeste, kob, the small antelopes and wild pigs, but in the immediate vicinity of the cattle-crossing continual disturbance keeps the game a short distance away. *Glossina tachinoides* is ubiquitous, but *G. palpalis* is absent. A belt of *G. morsitans* was found about eight miles distant, where the Morahgo River joins the Volta River and where there is a heavy concentration of game. *G. morsitans* has not been taken at this point on the cattle route, and affords an excellent example of natural control by disturbance of the game and the consequent driving back of the fly.

The head-waters of several streams arise on the dip slope of the scarp, and all have the same characteristic features. *G. palpalis* only is present and in considerable numbers throughout the year. The sandy soil does not support a tall vegetation, but bears a heavy growth along the streams, consisting of short palm trees (*Raphia vinifera*), bamboos, and stunted trees, of which *Linociera nilotica* is the most prevalent.

At Nagbo, twelve miles south, the predominant species is *G. palpalis*. *G. tachinoides*, however, appeared in small numbers from time to time, which suggests migration from a source lower down the stream. The vegetation is similar to that of the streams higher up.

From this point downwards the flora of the fly-belts becomes more luxurious, and at Jowani quite a heavy tree shade prevails over the stream, the plant association being changed by the appearance of several new species. *Morelia senegalensis* appears to be dominant, *Pterocarpus santilinoides* being also very common ; bamboo is still present, though not so prevalent as higher up ; *Sarcocephalus russeggeri* is conspicuous amongst the taller trees. The tsetse population shows more markedly than at Nagbo the seasonal incidence of *G. tachinoides*, whereas *G. palpalis* maintains steady numbers. The increase of *G. tachinoides* here in the early dry season occurs at the time of its almost total disappearance from the Nasia River.

South of Jowani, along the Kulda River, the vegetation consists of more extensive woodland, broken by patches of savannah, and game of every kind is extremely abundant. A belt of *G. morsitans* occurs, which impinges on the cattle route at a point one mile south of Jowani, where a tributary of the river crosses the route. The occurrence of this fly here is only sporadic ; it was first taken on both sides of the road in May 1929, but since then has not been caught upon the cattle road. It would appear then that only the fringe of this belt is involved, and that this species is not of economic importance as a vector of trypanosomiasis with regard to cattle at this point.

The vegetation bordering the Nasia River is typical of the flora produced on the clay shale formation of this region. This river, itself a tributary of the Volta, is the main stream draining the extensive area below the Gambaga scarp, and has cut a well defined channel with steep banks in the hard clay soil, but during nearly four months of the rainy season it overflows its banks and inundates large areas. The vegetation consists of a *Cynometra vogelii—Vitex cienkowskii* association and is remarkable for its extremely narrow and well defined limits, seldom extending more than twenty yards from the edge of the water and usually but five to ten yards in width. *Cynometra* forms the central zone, growing invariably close to or right in the water, and *Vitex* occurs in a regular fringe along the top of the river banks forming the outer zone of the vegetation. A number of other species of dense shade

trees occur, *Syzygium guineense* almost replacing the dominant *Cynometra* in parts. The vegetation is closely interwoven with a network of creepers and lianas, *Quisqualis indica* and *Paullinia pinnata* predominating. This matted and impenetrable growth produces a cavernous shade, which extends almost unbroken for the entire length of the river.

Kob, reedbuck, bushbuck, duiker, pig and warthog are very numerous along the river, and occasional herds of hartebeeste and roan antelope are found in the more open spaces; packs of baboons and troops of monkeys are ubiquitous; crocodiles and monitors abound on the river banks. In the height of the dry season (January to March) there is a general concentration of game along the course of the Nasia and its tributaries. From April to May onwards game is more widely dispersed, as soon as water and fresh grass are available at some distance from the rivers.

In April and May 1928, before clearing was commenced, both *Glossina palpalis* and *G. tachinoides* were caught at the ford where the cattle route crosses the river, the latter species being in the majority by more than two to one.

A belt of *G. morsitans* occurs at Baghale, west of the cattle road, extending up the valley of the Kulda River. To the east of the road, in the neighbourhood of some waterholes near Suguri and from there extending eastwards, this fly again occurs. The ever-increasing traffic on the cattle route has disturbed the game in the close vicinity, and it is possible that this is responsible for the division of what may once have been a continuous fly-belt.

Observations carried on when the Nasia River was being cleared showed very small numbers of *G. palpalis* in March 1929, but since then this fly has not been recorded here, although careful search has continually been made for several miles up and down the river. *G. tachinoides* exhibits the same remarkable seasonal fluctuation in numbers which has already been noted at the Tamne River.

Clearings on the Cattle Route.

As it was found that *G. palpalis* and *G. tachinoides* were the only flies of economic importance on this part of the cattle route, it was decided to clear the banks of the streams where these species were found. In order to facilitate the carrying out of the work by non-technical officers, a standard method was adopted for clearing at all points. The bush was completely cleared for a distance of half a mile along the river on either side of the point of the cattle crossing and the clearing was limited to a width of 20 yards on each bank. The work was undertaken by the District Commissioners in charge of the areas. A description is given of each clearing and of its effect on the incidence of the fly.

The Tamne River.

The Tamne River was cleared in March 1929. In July, when the river was getting full and grass was growing profusely throughout the clearing, no tsetse were found here, but only a short time was spent in searching. In September the river was very full, practically all the clearing was flooded, and grass had grown rank and high on the banks. Search for 10 days in both the cleared and uncleared areas resulted in the finding of only 6 *G. tachinoides* (4 males and 2 females) in the bush outside the clearing. During this year the cattle were not following this road, but were coming in from the Pusiga quarantine station.

In January 1930 no tsetse were found and there was little re-growth. In May 1930 the water was very low, forming a chain of pools. A prickly shrub, *Mimosa asperata*, was growing on the strips of sand in the river bed. The seeds of this plant, being water-borne, had been introduced from higher up the river and had established entirely new growth. Long grass was growing on the banks in profusion. Tsetse

were found at this date in quite large numbers, in two hours catching in the clearing 25 flies were caught, with a female percentage of 68; on the other hand in the uncleared portion a catch of 63 flies was made with a female percentage of 46. It would appear from the high female percentage found in the clearing that its fly population is very unstable. Most of the flies were caught in the shelter of the mimosa shrub, for which it seems to have a decided preference.

In January 1931, only 4 tsetse were caught in the clearing up-stream, and none could be found down-stream, a day's catching having been made at each place. Vegetation had increased slightly, a few stumps showing re-growth. There was still a fair amount of water in the stream bed. Very little farming at this point has been carried out by the local natives, as the wide-spread flooding prevents the cultivation of cereals, but some tobacco is cultivated with difficulty owing to the late subsidence of the water. The local population under the auspices of the District Commissioners was induced to cut away all the re-growth and leave it to dry. In conjunction with this cutting, grass burning is to be held up until the latest possible date, so that a fierce fire can be applied to the whole clearing simultaneously.

Kegbiri Clearing.

The alternative route entering by the Pusiga quarantine station is crossed by a branch of the Tamne River at Kegbiri. *G. tachinoides* was found here, and this was cleared at the same time as the Tamne River. The original fly population was very small and no replacement has been found in the clearing at any time. Re-growth of trees is slight owing to extensive flooding of the area, and tall grass prevents the encroachment of other plant life. Measures for maintaining the clearing, similar to those employed on the Tamne River, are being put into effect here by the District Commissioner.

Jelakolago Clearing.

This is also a tributary of the Tamne River. It flows swiftly, however, in a well-defined rocky and sandy channel and does not flood the surrounding terrain. Clearing was completed in February 1929. Farming of the cleared area was commenced in the following rainy season and has been continued during 1930, so that the whole of the cleared area is now under cultivation. This has had an excellent effect in keeping back encroachment of bush and re-growth of trees, and since the work of the clearing was finished no tsetse have been found here.

Nagbo Clearing.

The clearing was finished in March 1929, and was maintained free from vegetation by constant labour until June 1929. Only two tsetse were caught at this date during one week's observations on the clearing. These two male *G. palpalis* were taken under a clump of tall trees on the road 50 yards from the river, where travellers always rest. Further maintenance was stopped from this date and the grass was allowed to grow. When the clearing was visited in November 1929 farming had been commenced and about a quarter of the clearing was under cultivation; the remainder was under heavy grass, but there was no re-growth of trees, owing to careful stumping and burning. No tsetse could be found in the cleared area at all during this visit. Grass burning was delayed as late as possible. The next visit was in June 1930, and farming had been considerably extended, but no tsetse were found. By January 1931 the whole of the area was under cultivation with corn, yams, pepper, sweet potatoes, indigo and tobacco. It has been impressed upon the local people that the narrow strip of vegetation immediately adjacent to the river banks must be removed and kept under, and this measure is being carried out under the direction of the local chief.

Jowani Clearing.

Conditions are very similar to that of Nagbo clearing but farming has not been so extensive until recently, and a certain amount of fringing vegetation remained along the river bank. Immediately after the clearing was completed no tsetse were seen, but on subsequent visits a few were always found, invariably in close proximity to the river. The following table shows the actual catches :—

TABLE II.

Jowani Clearing.

Date	Where caught	*G. palpalis*		*G. tachinoides*		Average day's catch in uncleared river	
		♂	♀	♂	♀	*G. palp.*	*G. tach.*
16–19.vi.29	—	None		None		37	3
21.xi.29 ...	Clearing above ford ...	2	—	—	—	33	28
19.xi.29 ...	Clearing below ford ...	3	2	3	—		
26.v.30 ...	Clearing below ford ...	2	3	—	1	30	8
27.v.30 ...	Clearing above ford ...	—	—	1	—		
29.xii.30 ...	Clearing below ford ...	—	1	3	2	29	27
30.xii.30 ...	Clearing above ford ...	—	—	1	—		

The fact that tsetse were found in the Jowani clearing and not in the Nagbo clearing cannot be attributed entirely to the amount of farming. The unfarmed area covered with long grass was never found favourable to the fly, which was always caught along the stream bed and invariably more flies were present down-stream than up-stream. As Nagbo is situated close to the source of the river, whereas Jowani is mid-way between the source and the main river, the Nasia, it follows that at Jowani the up- and down-stream migration should be more apparent. This has been observed in the uncleared portion of the river, and probably explains the presence of tsetse in the clearing, which may be regarded as entirely transitory and the flies therefore of little importance as vectors of trypanosomiasis.

Nasia River Clearing.

Suguri, where the Nasia River crosses the cattle route, is the farthest point south which has been cleared. Clearing was commenced in December 1928, and finished by 21st March 1929. The cut wood and bushes were piled over the stumps of trees, which had been left along the river banks and burning was postponed until the end of April. A few large trees were left standing in the clearing, especially at the road crossing, where a small market is held, and at a place where a fish-trap is thrown across the river.

In April, a week after the clearing operations had ceased, tsetse were being caught in the clearing. By 10th April an average catch of 20 a day was being made. From this time onwards (13th–25th April), a total of 413 tsetse were caught in the clearing, an average of 34·6 a day. At the same time, however, it must be noted that the average catch along the uncleared part of the river was 66 a day. All the flies caught in the clearing were *G. tachinoides* and the female percentage was 65 as against 50 for the uncleared area. A very large population of flies caught in the clearing were young soft-bodied flies, which appeared to be hatching from pupae left in the ground undisturbed by clearing, but also breeding was taking place in the piles of brushwood, where the flies were finding sufficient shelter for existence.

The infection rate in flies in the cleared area in April was much lower than the rate in the previous months (see Table III), because of the number of young uninfected flies in the catch. On 26th and 27th April the cut vegetation of the clearing was burned, and for three days it appeared that the tsetse had all been driven out or killed by the fire, but on 1st May, 14 flies were caught in the clearing, showing a female percentage of 86. The number of *G. tachinoides* caught in the clearing rose

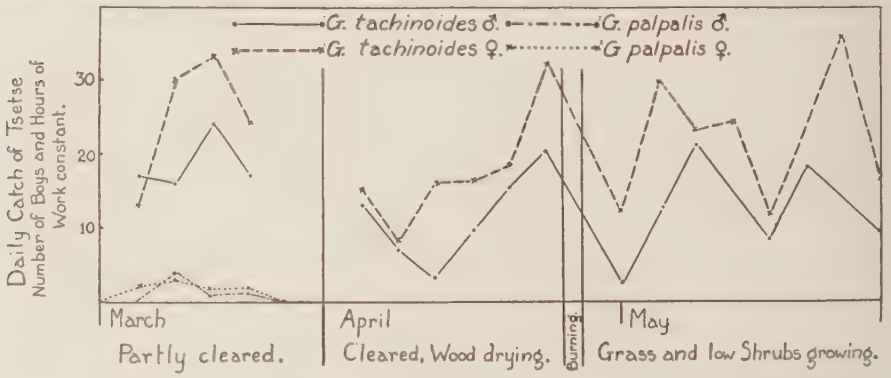


Fig. 3. Nasia River 1929. Effect of clearing *Cynometra vogeli—Vitex cienkowskii* association on *Glossina*.

rapidly, and during May, after 24 days' catching, the total number reached 877, an average of 35·7 flies a day. The female percentage remained approximately the same being 64·5. On the other hand tsetse incidence in the uncleared area had also reached a very high figure, 89 being caught in a single day. The female percentage was approximately the same as in the cleared area. In May the infection rate of flies in the clearing increased, owing no doubt to the decline in the number of young

TABLE III.

Blood Content and Infection of Glossina tachinoides *at Suguri.*

1929	Locality	Number examined	Number with blood	Percentage mammalian blood	Percentage reptilian blood	Percentage females with larvae	Percentage infection		
							T. vivax	*T. congolense*	*T. grayi*
March	River banks uncleared ...	63	15 (24%)	40%	60%	15%	3·2	3·2	12·7
March	River banks partly cleared	40	8 (20%)	33%	66%	13%	5·0	7·5	10·0
April ...	Clearing ...	160	25 (16%)	64%	36%	5%	2·5	1·8	1·2
May ...	Clearing ...	158	24 (15%)	75%	25%	12%	2·5	3·1	8·2

flies caught. The breeding-places had now been destroyed, and although the percentage of gravid females was higher, it is doubtful whether many of the larvae would find suitable places for pupation when dropped by the females. All likely breeding-places at the bases of trees and under stumps were searched, but no pupae could be found. Game was again visiting the clearing by the end of May and reptiles were common, affording an adequate food supply for the fly.

The reason for the continued presence of tsetse in the cleared area after burning was the fact that the burning was delayed until the first rains had fallen in April,

which resulted in the growth of a considerable amount of new vegetation outside the cleared area. This afforded shelter to the fly on dispersal. After burning, a re-growth sprang up in the cleared area consisting of grass along the edge of the river and certain tree-stumps which had not been killed; this afforded sufficient shelter for the fly, which then returned from its refuge in the environs. It is an important point that most of the captures were made under the tall trees and the shelter afforded by the sprouting stumps.

The clearing was again visited in November when a great change had taken place; the grass had grown profusely but the actual banks of the river were quite free from vegetation and all the stumps which were living and flourishing in May were now dead. In one place by the road a small farm had been made, but there had been no attempt at organised farming. An explanation can be given for the death of the vegetation along the banks. These riverside trees are physiologically very different from the trees of the orchard bush savannah country which are annually subjected to burning at the time of grass fires and have in consequence developed into a "pyrophytic" or fire-resisting flora. The riverside trees are never subjected to this burning, as the vegetation of these belts is always green and forms a barrier to the annual fires. Hence in the process of clearing, these trees were subject, first to the shock of cutting and mutilation and then to the shock of burning, which, although it did not kill outright all the stumps (many were sprouting green leaves in May) at least severely weakened them. They were then subjected to complete immersion for a period of about three months during the floods and were literally drowned. The aerial organs of the plant were gone and the roots were too weakened to be able to withstand so long a deprivation of oxygen.

No further re-growth took place from any of these stumps, as was proved by inspection in June 1930 (15 months after initial clearing ceased), and in December 1930, 21 months after clearing. On this last visit a new invasion by *Vitex cienkowskii* was observed at one place on the river banks, consisting of a few young bushes. These however have been cut. The continued freedom from re-growth of vegetation in the clearing of this river is in marked contrast to the happenings on all the other rivers, and is attributable to the thorough manner in which burning was carried out and more especially to the prolonged and extensive flooding of this river.

In November 1929 no fly was present in the clearing, but, as has been previously mentioned, *Glossina tachinoides* appeared to be absent from the Nasia River at this period of the year.

In June 1930, a few flies were caught in the cleared area. Six flies were caught in one whole day's searching; on the next day only two flies could be found. These were caught in the neighbourhood of the fish-trap and under the few remaining trees. Catching in the uncleared river produced 21 flies in an hour. Only *G. tachinoides* was found.

In December 1930 the clearing was again visited and no tsetse could be found either in the clearing or along the uncleared river, although an extensive search for four days was made. *G. palpalis* was present in considerable numbers at this point before clearing was undertaken, and was found in very diminished numbers until March 1929, while clearing was in progress, after which date none have been found on any part of the river in this neighbourhood.

Conclusions based on the Clearing Experiments.

We have found that when clearing has to be carried out at widely divergent points along a cattle road or a main trade route with the definite purpose of obtaining the maximum benefit for the project as a whole, not only is it necessary to make an intimate study of the fly community at each place, but the correct estimation of the plant community is of vital importance. This is well illustrated by the extraordinary divergence in the nature of the re-growth of vegetation in the clearings

and its effect on the re-establishment of tsetse. Two extreme cases, the Tamne River clearing and the Makongo clearing, may be cited.

On the former river, clearing was followed by no re-growth of any importance during the first year, but in the second year the introduction of *Mimosa asperata* along the river-bed together with a few shrubs and abundant long grass produced a cover sufficient to harbour considerable numbers of *Glossina tachinoides*.

At Makongo, eight months after the work of the clearing was finished, a low impenetrable re-growth of swamp-grass, shrubs and creepers had invaded the whole of the cleared areas, forming a plant community apparently inimical to the invasion of tsetse.

In contrast to these two examples there is a type of river, such as the Nasia, with a narrow band of vegetation which is subject annually to prolonged inundation. This factor, combined with clearing, has such an inhibiting action on the re-growth of the vegetation as to delay it for a considerable period.

In estimating the amount of clearing necessary at any place a study of the tsetse population itself is of main importance, and several factors must be considered as likely to influence the movement of the fly into the clearing. Such factors are :— (*a*) The density of the fly-belt ; (*b*) the amount of migration taking place up and down the river ; (*c*) scarcity of food ; (*d*) movement of hosts from uncleared river into the clearing.

In the clearings made on the Eastern cattle route the distance to which flies were found wandering varied greatly on the different streams, and it is considered that in some cases the extent of clearing might have been reduced with safety. In the experiments undertaken, which have been directed against *G. palpalis* and *G. tachinoides* only, the main object has always been the exclusion of the fly rather than the elimination of primary foci. Our clearings then must be regarded as palliative measures only, and to ensure their success we have invariably advocated the complete removal of all vegetation. On one or two occasions when a few tall trees were left any tsetse caught were invariably found close to or under them. It also seemed that the fly will use such trees as landmarks, flying from one to another, and will so traverse the whole of the clearing. Another argument in favour of the removal of all vegetation is that it exposes the ground to the maximum desiccation, which will tend to inhibit the re-growth of the typical moisture-loving flora of the fly-belt.

The importance of starting clearing operations as early as possible in the dry season cannot be too strongly emphasised. By starting work as soon as the subsidence of flooded rivers will allow, about November or December, the cut wood can be thoroughly dried and burned at least a month before the onset of the rains, so that stumps and roots not destroyed by burning will be subjected to the full desiccating effect of the dry weather before the first rainfall has given them a chance of recovery. Also, and of equal importance, this should obviate the continued existence of fly in the clearing as occurred on the Nasia. This of course only applies to areas such as the Northern Territories of the Gold Coast, where there is a long continued dry season. The laborious work of stumping a clearing is not essential on a river where extensive flooding occurs, as the combined effect of burning and flooding completely kills the vegetation. Otherwise it has been found very difficult to kill large stumps by burning alone, even when this is repeated in subsequent years.

When farming is undertaken after clearing, this is sufficient to prevent the encroachment of bush and re-establishment of tsetse, provided that the narrow strip of unfarmed ground along the river banks is kept free from vegetation. With the co-operation of the Political Department the cultivation of the cleared areas has been undertaken by the natives wherever it was possible, and the efficient and

enthusiastic way in which the local chiefs are now carrying out the policy is most encouraging. In several places farming is impossible owing to extensive flooding, and where this occurs there should be an annual cutting of any re-growth (except grass) found close to the river, and all burning should be delayed as late as possible.

Notes on the Bionomics of Tsetse in the Gold Coast.

Within the comparatively small area of the Gold Coast there occurs a great variety of natural conditions, climatic, geological, floral, and faunal, the outcome of which is to bring about the presence of a considerable number of species of *Glossina* of widely diverging habits.

The interrelation of these factors in rendering a particular locality suitable for a particular species of tsetse is of so complex a nature as to make the analysis of the individual requirements of any species a matter of the greatest difficulty. Climatic factors, for example, operating directly upon tsetse, are responsible for the seasonal distribution and dispersal of the fly ; but it appears as if their main influence is indirect, through their effect on vegetation, which has profound influence on the distribution of species and the localisation of fly-belts. This apparently direct connection between vegetation and tsetse may itself be secondary ; the governing factors may be the localised conditions of temperature, humidity, or light within the vegetational community. Certainly temperature and humidity seem the factors of greatest importance in influencing the metamorphosis of the fly in the pupal state.

Geology is a fundamental factor in determining the nature of the vegetation and by this means influencing the distribution of *Glossina*, but again this influence is indirect and in the localities under discussion we have no clear cases of the direct influence of soil upon the fly. There are certainly instances which look remarkably like a direct correlation between tsetse distribution and geological formation –for example, the band of *G. palpalis* that corresponds with the sandstone formation of the Gambaga Scarp ; but although the nature of the soil may be the fundamental factor, there are certain secondary and more superficial factors that actually govern the presence or absence of the fly. In other parts of the country *G. palpalis* is by no means confined to sandstone but is found occurring over the whole range of geological formations, from the mangrove swamps of the coastal rivers to the clay flats of the mid Volta basin.

As has already been observed, vegetation seems of primary importance in determining the presence of *Glossina* and the distribution of the species. This can be seen in an almost exaggerated degree in the savannah country of the Northern Territories of the Gold Coast, where the dry-weather fly-belts are often only 10 or 20 yards in width, owing to the narrow and abruptly demarcated bands of evergreen vegetation along the rivers. *G. morsitans* seems the most independent of vegetational factors, or possibly the more catholic in its range, its distribution being mainly influenced by food. In the case of *G. palpalis* and *G. tachinoides* a certain type of plant-community seems essential for the existence of the fly, but within this environment the distribution of these species seems to be determined largely by the presence of certain preferred hosts.

In the areas investigated—(*a*) the main cattle route from the French border to Kumasi, (*b*) the coastal plains of the Eastern Province, (*c*) certain portions of the true forest belt of Ashanti, (*d*) the fringes of the rain forest belt—the following species must be considered as being of possible economic importance :—(a) *G. palpalis, G. tachinoides, G. morsitans, G. longipalpis* ; (b) *G. palpalis* ; (c) *G. palpalis,* and possibly *G. fusca* ; (d) *G. palpalis* and *G. longipalpis.*

Glossina palpalis, R.D.

This is by far the most widely distributed species in the Gold Coast, occurring from the coast to the Northern border adjacent to the Haute Volta. It invariably affects the proximity of water or permanent swamps, wherever the vegetation is of such a character as to give sufficient shade and humidity. This species is very catholic in its choice of breeding localities as distinct from positions in which to drop its larvae. In the dry weather the most favoured locality for breeding is under the dense cave-like shade of the vegetation overhanging partly dried-up water-courses, but during the rains it will occupy isolated patches or bands of thick bush at considerable distances from the rivers. We are of the opinion that this habit of *G. palpalis* of making use of a great variety of environments for breeding and for forming wet-weather colonies has led to its wide dispersal and distribution throughout the country. Within the breeding area this species appears to exert a definite choice of positions in which to drop the larvae, and in many instances we have found a few large fallen logs alone to be selected in quite a considerable area, as many as 60 pupal cases having been found under one log. In laboratory experiments the average period between the depositions of larvae was found to be 10 days, the variation being between 6 and 17 days. Breeding is mainly confined to the rainy season.

In the seasonal incidence of adults there is a steady increase in numbers from the beginning of the rains onwards, culminating in the maximum density in September, after which there is a steady fall to the minimum numbers about January (see fig. 4). This sequence of events has been observed in savannah forest type of country, and it will probably differ slightly in rain forest and in coastal savannah, where there is a different distribution of rainfall through the year.

G. palpalis is an omnivorous feeder, and although wild animals may be considered its normal hosts, it seems very ready to leave these when there is an abundant and readily available supply of food in man and domestic stock. This leads it to form concentrations around fords, water-holes, and riverside villages. Our observations on the distribution of this species lead us to believe that in certain areas man is definitely the preferred host. We have also noticed this species to be very prevalent in the vicinity of the schools of hippopotami, and on shooting one of these animals numbers of tsetse were observed attacking the softer portions of the carcase, such as the nostrils, ears, and genital organs. These animals occur in the quieter stretches of the rivers where there is an abundance of game, which might also be the reason for the increased incidence of the fly.

In the more thinly populated coastal area of the Eastern Province of the Colony the food supply of *G. palpalis* consists of the numerous droves of semi-wild pigs which frequent the streams, cattle and man at the water-holes, and occasional reptiles.

Glossina tachinoides, Westw.

G. tachinoides may be designated as an "up-country" species, being confined to the savannah country of the Northern Territories. It has not been found in the forest and appears to be absent from the coastal savannah of the Eastern Province of the Colony. It is essentially a riverside species, but given the presence of water it seems able to survive in quite open country and in the presence of comparatively little shade. The localities in which it is found breeding appear to be restricted to the close vicinity of rivers and streams, but within these areas the pupae are found more widely scattered than those of *G. palpalis* and the fly does not appear to favour any particular position in which to deposit larvae. We have found pupae in the debris in the forks of trees, four feet up from the ground. On less heavily wooded rivers pupae have been found under the shelter of overhanging rocks. In wet weather it will live and breed in localities with very scanty cover, but one condition has been found essential for this, the presence of high shade as well as low cover.

Without both of these factors neither temporary nor permanent fly-belts can be formed, although this species will wander for very great distances across open country or along open water-courses during the wet season. Its range of flight in this respect probably exceeds that of *G. palpalis*.

In contrast to *G. palpalis*, which is inclined to spread outwards from the river in the wet season, this species undergoes extensive migrations along the main rivers or up side-streams, thus forming secondary wet-weather fly-belts in localities many miles from the primary foci. Evidence of this movement has already been quoted in the description of the fly-belts at Mogonori, the Tamne River, and Jowani. Another means of dispersal is effected by the fly following its hosts. We have observed cases of *G. tachinoides* and *G. palpalis* following cattle for two miles in open orchard-bush country at Makongo, and of *G. tachinoides* following cattle for three and a half miles in similar open country in the Gambaga district. This was at the driest time of the year, when the shade temperature at mid-day was 91 F., and the relative humidity of the open bush was 22 per cent.

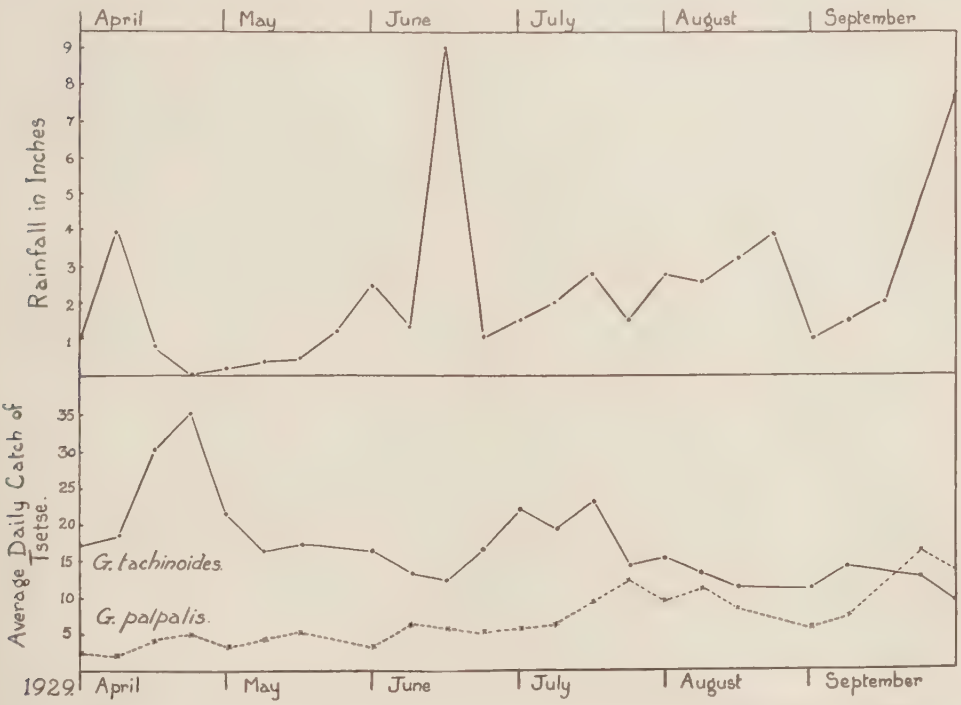


Fig. 4. Rainfall and seasonal variation in incidence of *Glossina* on the River Volta at Yeji.

This species is liable to extreme fluctuation in numbers, this being mainly seasonal, but by no means regularly so, and a marked annual variation in incidence has been noticed. The usual course of the seasonal incidence of *G. tachinoides* is as follows: A very small population during the height of the dry season (Christmas time), but these flies are actively breeding. At the onset of the first rains (end of February or in March) a great hatch of pupae causes a tremendous increase in numbers. The length of the pupal period is markedly affected by atmospheric humidity so that pupae deposited early in the dry season and those deposited late all appear to hatch out at about the same time, when rainfall causes an increase in atmospheric humidity.

This increase in numbers of *G. tachinoides* continues throughout the early tornado season, April, May, and June, but by the time the heavy rains set in, about July, there commences a steady diminution in numbers, which is brought about by flooding, which disperses the fly and drives it out of its primary centres, where breeding is now impossible or suitable places are very restricted. Thus the end of the rains finds a population of this species much reduced in numbers. This picture is, of course, not universal, but it shows the general sequence of events on most of the rivers in the Northern Territories where *G. tachinoides* is found. Fig. 4 illustrates graphically the fluctuation in numbers of *G. tachinoides* as observed on the River Volta at Yeji throughout six months of the wet season in 1929. The first rains in April brought about a very great increase in numbers due to the emergence of young flies. A greater rainfall in June was accompanied by a lesser increase in the fly, and as the wet season progressed the steady reduction in numbers that took place swamped any temporary increases due to hatching.

From our observations we have gathered the impression that *G. tachinoides* prefers wild game and reptiles as hosts, and does not prefer men and domestic animals when a plentiful supply of other food is available. In its distribution it is found in greater numbers in the remoter and wilder bush away from villages where wild animals are the only possible source of food. The driving away of game, however, does not seem to affect it very much, as it will readily feed on reptiles and probably the smaller mammals ; indeed, in some places it seems as if this fly favoured a reptilian diet. Evidence of this has been noticed under our description of Mogonori. At the Nasia River for two months after clearing, game, formerly abundant, was driven right away, but plenty of crocodiles and monitors remained along the cleared river and the flies found in the clearing must have been dependent upon these for their food supply. In many cases where even the smallest varieties of game are conspicuous by their absence, but where crocodiles and monitors are plentiful, *G. tachinoides* has been found in considerable numbers. Such localities have been observed on the Red and White Volta Rivers in the north of the Kusassi district, on the Tamne River, and on the Morahgo River. On such rivers the fact of the flies frequently being found close to the water's edge sheltering in the scantiest of cover may be explained by their seeking reptilian food.

Glossina morsitans, Westw.

G. morsitans is the only species of tsetse which has been found to feed almost exclusively on one class of host, the larger antelopes, and this appears the main factor influencing its distribution in this country. Wherever we have found this species it has been in the presence of the larger game animals, and a scarcity of these, or even the disturbance of the game, is sufficient to bring about the disappearance of this tsetse. Instances of this have already been quoted in our description of the fly-belts on the cattle route, but an even more striking example is found in the way *G. morsitans* has disappeared along the Main North Road from Tamale to Kumasi. We have ample reliable evidence that formerly infestation by this fly was quite heavy and that game was abundant in many parts of the country close to the road, notably between Ejura and Prang ; all along the wide valley of the Volta basin, this affecting the road in the neighbourhood of Yeji and Makongo ; and from Salaga to Yamallaga, not far from Tamale. In 1927 this species could be found nowhere along the main road, though it was taken around Makongo and occasionally following cattle half a mile or so from the road. More frequently it was captured in the good game country along the Volta three or four miles or so from the road. In 1928 none was caught in the neighbourhood of Makongo, only in the remoter bush. In this locality in 1930 the only flies of this species were captured 15 miles up the river from Yeji, and here they were not numerous. At this time the larger species of game were becoming scarcer every year throughout this tract of country owing to the depredations of the innumerable native hunters, both local

men and natives who come up from Ashanti with the object of shooting all the game they can and drying and selling the meat. Also the heavy motor traffic, by disturbing the game in the neighbourhood of the road, has been a material factor in the reduction of the fly.

The vegetation we have found most favourable for permanent fly-belts of *G. morsitans* is of the woodland savannah type consisting of open grassy glades surrounded and interspersed with belts and thickets of tall evergreen trees, usually without much dense low cover but giving ample shade themselves. Such vegetational communities most usually occur along river valleys and in country with a light sandy soil with permanent subsoil water. The presence of surface water is by no means essential to the fly, although it is true that concentrations of *G. morsitans* have been found round isolated water-holes in perfectly open country. Here the presence of game is the main attraction however.

The fly-belts of *G. morsitans* in this part of the country do not seem to have very well defined limits, owing to the habit of the fly extending its range, not as single individuals but often in numbers, well outside what at first seems to be its primary focus. This occurs both in wet and dry seasons, and again this seems mainly brought about by the movements of game. When investigating the *G. morsitans* fly-belt along the White Volta River below the Gambaga Scarp in June 1930 (early rains) no flies could be found above the scarp. When this place was visited after the wet season, in January 1931, quite a heavy concentration of this species was encountered in very open, rocky, scrub country on top of the scarp, only 4 or 5 miles north of Gambaga. This was a very dry time of the year, the shade temperature in the open here being 94° and the relative humidity 19%. Game was abundant at this place at the time. Undoubtedly this was a part of the larger fly community below the scarp. It has been noticed that game ascend and descend the escarpment here, and it is probably in this way that the small community of fly got isolated during the preceding wet months when game movements were extensive.

Nowhere have we found this fly in sufficient numbers to warrant much time spent in searching for pupae, but they have been taken on rare occasions at the mouths of large ant-bear holes and in porcupine holes.

Glossina longipalpis, Wied.

G. longipalpis has not been found on any parts of the Eastern cattle route in the Northern Territories, but is common in many places on the western side and in parts of Ashanti. It has been found within ten miles of Accra itself, where vegetation commences towards the rising hills, and also around Sekondi and Takoradi. Its habitat appears to be the dense thick secondary bush, intermediate between the true forest and savannah country, and in its distribution it has not been found occurring in either of these latter types of country. We have observed that it is always associated with a considerable incidence of the smaller antelopes, which undoubtedly form its chief supply of food. In this respect its biology approaches that of *G. morsitans*.

Glossina medicorum, Austen.

This large and interesting species was found in the dense shade of the thickets and tall trees fringing the River Volta at Yeji. It is not really abundant here, but 30 to 40 specimens were taken from time to time during six months. It was observed following the cattle for three-quarters of a mile from the river banks, but it is very local in its distribution. We have since found it in small numbers at Takoradi, in secondary bush, an entirely different type of vegetation from that which we originally considered its normal habitat. The pupae were found under large logs together with those of *G. longipalpis*, in the tall and heavy vegetation on the banks of the River Volta.

Glossina fusca, Walk.

This is essentially a forest species and is fairly abundant along the forest paths and at the edges of clearings.

Glossina nigrofusca, Newst.

This species appears to have the same habitat as *G. fusca*; it has been reported from Sungani, but does not appear to be very common.

Glossina pallicera, Bigot.

This appears to be a forest species and is distinctly rare; recorded by Dr. C. M. Ingoldby, near the Birrim River in the Western Province of the Colony.

Glossina caliginea, Austen.

This species appears to be very rare and has been taken once at Nsuta near Kumasi, in the thick forest of Ashanti. It was found near a small stream.

Acknowledgments.

We welcome this opportunity of acknowledging the co-operation and help given by the Veterinary Department during the investigations, and of thanking the officers of the Political Department for their invaluable assistance in the work of clearing. We are indebted to Mr. C. Vigne, of the Forest Department, and Mr. L. Williams, of the Agricultural Department, for their assistance in naming botanical specimens. Our especial thanks are due to Sir Guy Marshall, C.M.G., F.R.S., Director of the Imperial Institute of Entomology, for his continued advice and help throughout the course of the work.

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APPENDIX.

AN ECOLOGICAL STUDY AND EXPERIMENTAL CLEARING AT MAKONGO.

By K. R. S. MORRIS, B.Sc., A.R.C.S.

The village of Makongo, on the Kumasi-Tamale main road six miles north of Yeji Ferry, had been found by the pathologist at Yeji to be an endemic sleeping

sickness centre, and in 1930 an experimental clearing of the fly-belts around Makongo was undertaken.

Mr. Pomeroy had already made investigations into the tsetse problem here during 1927 and 1928. The writer made a preliminary tsetse survey in January 1929, and in January 1930 undertook a rather more detailed ecological survey, advised as to measures for clearing, and carried on observations on the effects of the clearing.

Physical Features of Makongo.

Makongo lies just at the edge of the flat open savannah country which forms the basin of the Volta River. The impervious clay soil of this area is subjected annually to considerable flooding, but is baked hard during the dry season. The town itself however is situated at the point where the sandy soil of the higher ground overlies the clay strata, producing a fertile area with a rich subsoil and a permanent supply of water. The Makongo River, a tributary of the Volta, skirts the town to the south.

In consequence of the geological formation the flora here is richer than in the surrounding terrain. The river, where it flows over the flat clay soil, is fringed with the dense shade-giving *Cynometra vogelii*–*Vitex cienkowskii* association which has already been described as occurring on the Nasia River. Close to Makongo, where the sandy soil impinges upon the river, there is a heavy growth of *Ficus congensis* covering 600 yards of the river banks. To the north, south and west of the town within a few hundred yards is permanently swampy ground with a tall woodland vegetation of trees 80 to 100 feet high and a thick undergrowth of shrubs and swamp grass.

The open savannah grassland of the plains south of Makongo is broken by stretches of orchard bush and occasional thickets of *Sarcocephalus russeggeri* and clumps of low thorn bushes. The higher ground north of Makongo is uniformly clothed with orchard bush savannah.

The plant associations of the sandy river bank and swamp were studied by making a count of trees within a strip 100 yards long by 10 yards wide. By the river the vegetation rarely extended more than 10 yards from the water's edge, so the whole of the flora of one bank for a length of 100 yards is included in the count. The figure in brackets after the name of the species indicates the number of trees found in 100 yards.

Ficus congensis (12).—The dominant tree of this community; the number does not indicate its true position. Each individual consists of a long horizontal trunk from which spring several upright stems, and there are innumerable thick aerial roots forming deep cave-like shelters beneath the trunk. The tree grows right in the water, the trunk extending 3 to 4 yards up the bank thus covering a considerable area. The range of this species seems limited to sandy soil.

Pterocarpus santalinoides (16).—In the dense shade of the *Ficus* this tree was small and straggling, elsewhere it attains a large size. Always close to or in the water. Limited to sand.

Cynometra vogelii (6).—This tree, the dominant on the clay soil, cannot compete with the *Ficus* and was only found here sparingly at the edges of the thick vegetation.

Vitex cienkowskii (4).—Associated with above species on clay soil, this tree also was poorly represented here, growing only in the more open parts.

Syzygium guineense (3).—A fairly large spreading tree, found only at the edge of the vegetation here, numerous elsewhere on the river.

A low-growing evergreen shrub, *Cephaelis* sp., was very common under the shade of these trees, forming a dense low shade. Creepers and lianas formed a tangled growth over the lower branches of all the trees, the predominant species being

Paullinia pinnata and *Quisqualis indica*. There was a transition zone between the *Ficus congensis* and the *Cynometra vogelii–Vitex cienkowskii* communities in which *Pterocarpus santilinoides* was the dominant tree. The *Cynometra* community on the clay soil was even more limited in extent than the *Ficus* community, forming a very narrow strip of vegetation from 3 to 6 yards wide and 20 to 30 feet high along the river banks. In places the banks were quite open, or clothed only in a low growth of *Quisqualis indica*.

The woodland around Makongo was more extensive in area than the river-side communities, the band of vegetation being never less than 100 yards in width. A typical strip 100 yards long by 10 yards wide examined contained the following trees :—

Isoberlinia doka (20).—The dominant tree, tall and strong-growing, forming the upper high-shade layer. Evenly distributed throughout.

Ouratea flava (18).—A low laurel-like bush forming an under storey of low shade. Abundant everywhere except in very wet waterlogged ground.

Raphia vinifera (20).—This palm was very numerous in parts, growing in clumps around the pools and streams.

Elaeis guineensis (15).—The palm from which wine is obtained. Also growing in clumps, but on drier ground than that affected by the above species. The ground at the base of these palms was much favoured by *Glossina palpalis* for breeding.

Pterocarpus santilinoides (10).—Growing to a tall tree in this community, this species occupies the more central wetter zone.

Syzygium guineense (8).—A tall spreading tree, occurring in the drier outer zone.

Terminalia sp. (7).—Habits like *Syzygium*.

Diospyros mespiliformis (6).—This attained a large size and usually grew on the tops of old termite mounds. Always well covered with creepers. The loose soil around the roots of this tree formed an admirable breeding-place for *Glossina palpalis*, especially when the lower ground was flooded.

Sterculia tragacantha (6).—A tall, slender tree giving high shade. Most of the individuals were saplings.

Vitex cienkowskii (5 or 6).—This only grows to a small size and occurs sparingly.

Ficus capensis (5 or 6).—Fairly common, small growing tree, occurring in more open parts.

Pterocarpus erinaceus (3).—Found only at the edge of the bush.

Cephaelis sp.—Occurred also in this community, on parts of the drier ground, forming a dense low shade layer, 1 to 2 feet high.

A coarse swamp grass with very sharp cutting leaves grew plentifully where there was open water. Creepers and lianas were ubiquitous and of many species, most of which could not be identified. *Manniophyton africanum* was noticeable as making dense green canopies over the low shrubs, forming excellent cover for tsetse. To the south of the village was a mixed association consisting of typical *Isoberlinia doka* woodland with an introduction of *Ficus congensis*.

The plant communities described above constituted primary fly-belts, with tsetse present and breeding throughout the year. Secondary fly-belts exist around Makongo in which tsetse were not found until the rainy season had started in March, but from then until the following dry season they are occupied by small colonies of the fly. On the sandy soil such secondary fly-belts were of the woodland vegetation type —with *Pterocarpus santilinoides* the dominant tree, other species of tall trees (unidentified), both species of palm and a scanty undergrowth of grass and creepers. Surface water was usually absent, though the ground was moist even at the height of the dry season.

Small thickets of *Sarcocephalus russeggeri* were found in the orchard bush savannah on the clay soil, and also another type of small thicket formed by one or two large ebony trees (*Diospyros mespiliformis*) situated on an old termite mound and surrounded by a fringe of low thorn bushes. At the onset of the rains when the verdure was springing up both these types of thickets were occupied by *Glossina palpalis* and it is probable that this fly remains and breeds in these situations during the wet season ; the point however has not yet been proved.

Shade Temperature and Humidity.

In the main plant communities round Makongo readings were taken with a wet and dry bulb hygrometer to ascertain shade temperature and relative humidity. Unfortunately a whirling type of hygrometer was not available, and relative humidity estimated with a stationary instrument is not accurate, the error involved being greater, the greater the depression of the wet bulb, so that at high humidities this is very small indeed. As however a considerable difference was found between the humidities of different types of vegetation, the figures are given as having at least a comparative value.

The *Cynometra-Vitex* and *Ficus* communities of the river banks were practically identical in their range of humidities and shade temperatures, and only one set of figures (for *Ficus* community) is quoted, for comparison with *Isoberlinia* woodland and open orchard bush. Readings were taken at mid-day, and at a uniform height of two feet from the ground, the height at which tsetse have been commonly found settling and flying.

TABLE IV.

Noon Relative Humidities and Shade Temperatures at Makongo, Jan, 1930.

January 1930	Open orchard bush ; no tsetse		*Isoberlinia doka* community		*Ficus congensis* community	
	Shade temp.	Rel. humid.	Shade temp.	Rel. humid.	Shade temp.	Rel. humid.
	°F.	%	°F.	%	°F.	%
18th	91	30	80	56	84	51
21st	94	50	88·7	56	85·5	59
25th	95	15	83·7	37	87·5	29
29th	94	16	85·2	24	89·5	20
31st	90	22	83·6	50	86	30
Average	92·8	26·6	83·2	46·6	86·4	37·9

The greater relative humidity of *Isoberlinia* wooding in comparison with *Ficus* bush is due both to its denser nature and to its much greater extent. The narrow band of river-side vegetation is rapidly dried by a strong wind, and very low humidities (16% and 17% R.H.) have been recorded in similar fly-belts under such conditions. The considerable day to day variation in humidity was due to a cool dry wind from the north, the harmattan, which blows intermittently at this season.

These observations on the normal plant community could not be continued, as clearing commenced in February. The effect of clearing was to produce an immediate rise in temperature and fall in relative humidity, but this latter was soon nullified by the first tornado on 22nd February (1·05 inches of rain) and another on the 28th

February (0·9 inches), which caused a considerable rise in general atmospheric humidity, and the relative humidity of the cleared areas and open bush now approached more closely the humidity of the uncleared vegetation. A typical set of figures is given.

TABLE V.

Effect of Clearing on Shade Temperature and Relative Humidity at Makongo.

27th February	Open bush	Clearing by river	Uncleared fly-belt *Cynometra-Vitex* association
Relative humidity ...	65%	69%	71%
Shade temperature ...	88°F.	88°F.	84·5°F.

As a rule there was a more marked difference in shade temperature than is shown in this table, the temperature of the open ground remaining constantly higher than that of the fly-belt.

During February the average relative humidity for the month was 46% for open bush, and the average for March was 50·2%. During the first week in March it was noticed that tsetse were following along paths and into open country away from the river at Makongo, whereas hitherto the fly had been confined strictly to the shelter of the thick bush. On 15th March it was very noticeable that both *G. palpalis* and *G. tachinoides* were leaving cover and coming out into the open to attack passers by. This was at a spot down the Makongo River where a well worn game-path skirted the river within 10 to 20 yards, and here undoubtedly the fly were accustomed to procure their meals by dashing out to passing animals. The fly followed the writer at least half a mile into the bush on several occasions. On 17th March some of the outlying thickets of *Pterocarpus santilinoides* and palms mentioned were found harbouring one or two *G. palpalis* where no fly had been found previously. By the end of the month this species was quite numerous here. At this place the palm trees were being cut for wine and it was visited daily by a man who had to pass a heavily infested fly-belt on the way. In this manner tsetse would be introduced into this secondary fly-belt.

TABLE VI.

Average Noon Relative Humidities and Shade Temperatures at Makongo, Dec. 1930.

Average 10th–16th December 1930	*G. palp.* & *G. tach.* present	*G. palp.* found on two occasions	No Tsetse		
	Cynometra-Vitex association	Re-growth in clearings	Open clearing, re-growth cut	Secondary fly-belt	Open grassland
Relative humidity ...	67·1%	69·6%	58·3%	60%	59%
Shade temperature ...	87·7°F.	89·8°F.	90°F.	89°F.	92·1°F.

In December 1930 some further observations were made on relative humidity and shade temperature at Makongo, using the whirling psychrometer for estimation of the relative humidity. *Isoberlinia* and *Ficus* communities had all been removed by clearing previously, so the *Cynometra-Vitex* association was taken as a typical fly-belt. A week's consecutive readings were taken at the following points, and the

average relative humidities and shade temperatures are given in Table VI: (1) *Cynometra-Vitex* fly-belt, in which *G. palpalis* and *G. tachinoides* were always found; (2) open grassland within 20 yards of (1), where no tsetse were ever caught; (3) a secondary fly-belt which was not now populated with fly; (4) the dense re-growth in the cleared areas, where *G. palpalis* was found in one spot only on two occasions; (5) the perfectly open clearing in which the re-growth had been cut and no tsetse were ever found.

The daily variation in humidity and shade temperature for the fly-belt and open grassland are represented graphically in fig. 5. No fly were found wandering into the open at this time, yet it is noticeable that, even in the short period covered by these observations, the relative humidity of the open ground varies well within the lower limits of the fly-belt's humidity. This same phenomenon is more marked in the table for January 1930.

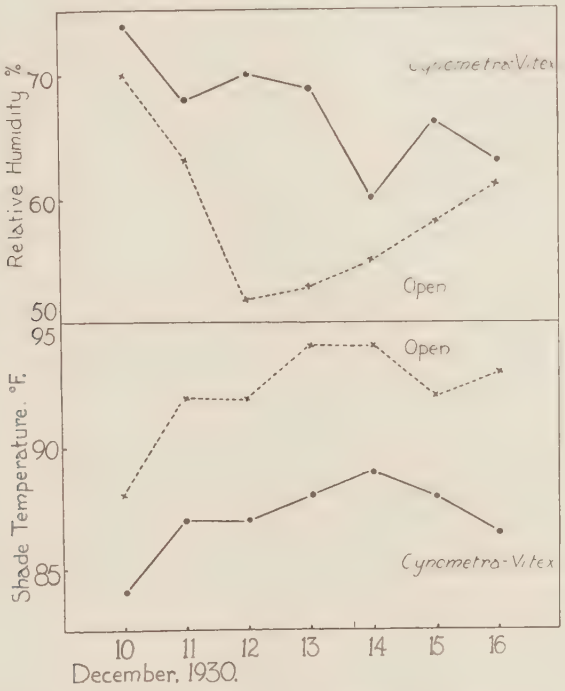


Fig. 5., Makongo. Shade temperature and relative humidity of *Cynometra-Vitex* association fly-belt and open grassland, Dec. 1930.

It appears then that the fly always tends to move into the places of greatest relative humidity, and it will not move out of these places until the general atmosphere has reached a certain degree of humidity which is far higher than that at which the normal life of the fly is possible.

Food of Tsetse at Makongo.

The grass savannah of the Volta basin has a considerable fauna of all varieties of wild game, and these approach close to Makongo and have regular drinking-holes along the Makongo River during the dry season. The larger antelope are not seen so frequently in this area as they were a few years ago, having been driven back by the disturbance of continual traffic on the motor road and also by the native hunters,

who continually harass the game in the vicinity of every town. In January to June 1930 the following animals were recorded within a half-mile radius of Makongo, this radius embracing all the fly-belts whose plant communities have been dealt with above :—

Kob (*Adenota kob*) were frequently seen along the Makongo River and were using regularly a drinking hole a quarter of a mile west of the town. A pair of bush-buck (*Tragelaphus scriptus*) frequented the *Isoberlinia* woodland west of the town, and another pair the patch of woodland to the east. Duiker (*Silvicapra grimmi* and *Cephalophus rufilatus*) were frequent visitors to the farms close to the town. Reedbuck (*Redunca redunca*) and hartebeest (*Alcelaphus major*) occurred to the north just outside the half-mile radius. Small FELIDAE were common and included serval (*Felis serval*), marsh mongoose (*Atilax paludinosus*) and a genet (*Genetta pardina*); although these three species are nocturnal, their habit of lying up during the day in thick bush would make them readily available to tsetse. Baboons were frequently seen in the woodland to the north and east of Makongo, or ranging over the open country. Large numbers of fruit-bats rest in the heavy shade of the river-side bush ; it is uncertain whether these do form a source of food for tsetse, but they were certainly very available to the fly. Rodents were ubiquitous, and the large " cutting grass " (*Thryonomus* sp.) occurred especially in the wetter ground by the river and streams. Small crocodiles and monitors were very common along the river, and in the wet season were found wandering some distance from the river. Birds are in great variety and abundant in this locality, but they are more likely to be predators than prey, especially the small bee-eaters, of which a small colony lived close to the town.

It will be seen that the wild fauna in the neighbourhood of Makongo was probably sufficient in itself to support a considerable population of tsetse, but there was, besides, a considerable source of food in humans and domestic animals. The population of Makongo itself is small, but it is a market centre of local importance which brings in people from the surrounding villages. It is situated on the eastern cattle route and the main motor road, so that there is a continual stream of travellers and traders passing through, most of whom stop in the town to buy food and to rest, and drink and wash at the river. Herds of cattle invariably sleep at Makongo, in order to be able to cross the Volta six miles south early the next morning. The cattle road skirted closely the *Isoberlinia* woodland and the riverside *Ficus* bush as it passed Makongo (Map 2). All the washing and drinking places used by the local people and strangers were closely surrounded by dense bush. From the distribution of tsetse it appeared that this regular and abundant supply of human and cattle hosts available to the fly might be of more importance to it than the wild fauna.

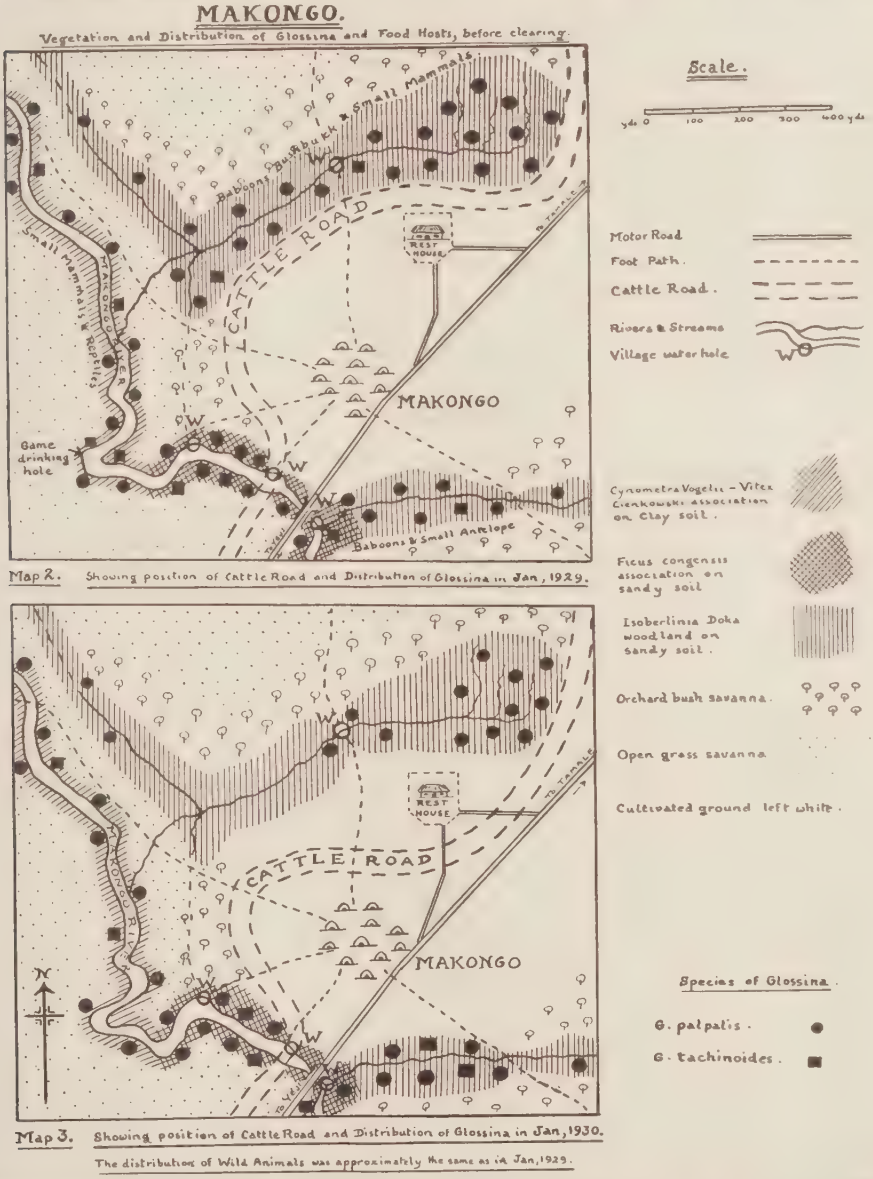
The Species of Tsetse and their Distribution.

Five species of tsetse were recorded from Makongo by Mr. Pomeroy in 1927 and 1928. They are, in order of abundance :—*Glossina palpalis, tachinoides, morsitans, longipalpis* (a single specimen) and *medicorum*. The last two were probably of accidental occurrence and were only found on one or two occasions.

In 1928 *G. morsitans* was not found in the neighbourhood of Makongo, and the writer has not found it there during his work in 1929 and 1930. The disappearance of this fly can most certainly be correlated with the growing scarcity of larger game animals in the close neighbourhood of the town.

G. palpalis is the most abundant species here at all times of the year, and is distributed along the Makongo River in the *Cynometra-Vitex* and the *Ficus* associations, and throughout the *Isoberlinia* woodland. It has been found breeding in all these communities. A remarkable difference in the distribution of this fly was observed between January 1929 and January 1930, a careful and detailed survey having been made at both of these times. This is illustrated in Maps 2 and 3 of Makongo, and the

difference in the distribution of the fly can be correlated with a slight change in the cattle route. In 1929 the cattle route skirted closely the *Isoberlinia* woodland north and north-west of Makongo, giving ample opportunity for tsetse in this fly-belt to feed upon the passing herds; *G. palpalis* was evenly distributed throughout the



Isoberlinia woodland, and an occasional *G. tachinoides* was found. In January 1930, when Makongo was next visited, *G. palpalis* was found only in that part of the *Isoberlinia* woodland immediately north of the rest-house, and around the small water-hole to the north of Makongo. No tsetse could be found in the bush immediately west of this spot, where formerly they had been abundant. It was noticed

that the cattle were now following a route south of the rest-house, and the only place where they approached closely to the fly-belt was where the road skirted for a short distance its extreme eastern limit. So far as could be ascertained, the distribution of wild animals was very much the same during the time of these observations. It appears from this that cattle and human hosts outweighed all the other hosts in their influence on the distribution of *G. palpalis* at this particular place.

In January 1930 *G. palpalis* was more abundant in the *Isoberlinia* woodland than in the riverside communities, the average daily catch in the former place for the month being 29 (female percentage 42), as against an average daily catch of 20·8 (female percentage 37) in the *Ficus* community. The higher female percentage in the former indicates a less stable community and it will be seen that this was confirmed by the effects of clearing. (In making these catches the same four boys were always employed and worked for only 4 hours during the hottest time of the day, when tsetse were found to be most abundant.) During the rains *G. palpalis* wanders far from these primary foci, and establishes itself in small secondary colonies. This has been described above (p. 520).

G. tachinoides occurs permanently only along the Makongo River, although numbers were caught in the small patch of *Isoberlinia* woodland immediately south of the town, but it was not breeding here. It is never so abundant as *G. palpalis*, the proportion between the species showing a seasonal variation. In the height of the dry season *G. palpalis* outnumbered *G. tachinoides* by 3 to 1 along the river, and in the patch of woodland just referred to by 4 to 1. At the end of the dry season and as the rains commenced (end of February and in March) the proportion became less, approaching 2 to 1, and by May and June, when the rains had really set in, the two species were being caught in very nearly equal numbers, but still with *G. palpalis* showing a slight predominance. Towards the end of the rains there is a steady falling off in the numbers of *G. tachinoides*, but the decrease does not become marked until the dry season has set in, about Christmas time. There is indication of an annual variation in the relative abundance of these species, but sufficient consecutive observations have not been taken as yet to show to what extent this occurs.

The Clearing Experiment.

The aim of the Makongo clearing experiment was to test the efficiency of a minimum amount of clearing in excluding tsetse from the village and village watering-places and to execute this clearing at a minimum expense, putting into effect the experience gained from the observations on the cattle road clearings. The standard of clearing laid down was the removal of all primary tsetse foci occurring within a quarter of a mile of the town, and the removal of all heavy bush within 100 yards of watering-places. As with the cattle road clearings, all vegetation, both trees and undergrowth, was cleared. Even this standard involved a large amount of clearing owing to the presence of the exceptionally dense woodland to the north, west and south of Makongo. In all, 20 acres were cleared, of which 16 acres were *Isoberlinia* woodland and only 4 acres of riverside *Ficus* community.

Clearing operations started at the beginning of February 1930 and clearing and burning was finished by the end of March, the work being in charge of Mr. Cooper, Assistant District Commissioner. Owing to the early rainfall this year the work of burning the stumps and roots was very difficult, and in the *Isoberlinia* woodland especially many were left unburned and were sprouting new foliage in April, and by June there was a fairly profuse re-growth in all the clearings. Despite this the effect of the clearing was to drive out *G. palpalis* almost at once from the cleared *Isoberlinia* bush, and to these areas the fly never returned. Fig. 6 shows graphically the effect of clearing the the *Isoberlinia* woodland north of Makongo. The few flies that were caught in this clearing during April, May and June, were always found close to a water-hole which was being used constantly by natives from the village.

The enormous rise in the female percentage of the catch upon the commencement of clearing is difficult to explain, unless it is assumed that this was a favoured breeding area with a high proportion of breeding females which would not be caught in the ordinary course of events.* The same phenomenon was observed, but to a less

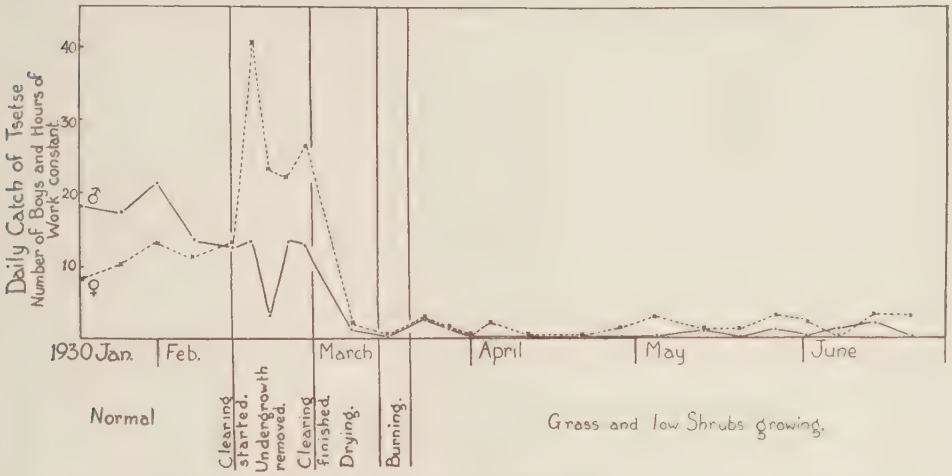


Fig. 6. Effect of clearing *Isoberlinia doka* woodland on *Glossina palpalis* at Makongo.

extent, when the riverside *Ficus* bush was cut, and also during the clearing on the Nasia River in 1929. This high proportion of females continued in the catches made in the clearings throughout the time of observation. It is certainly indicative of disturbance in environmental conditions and probably of hunger in the fly.

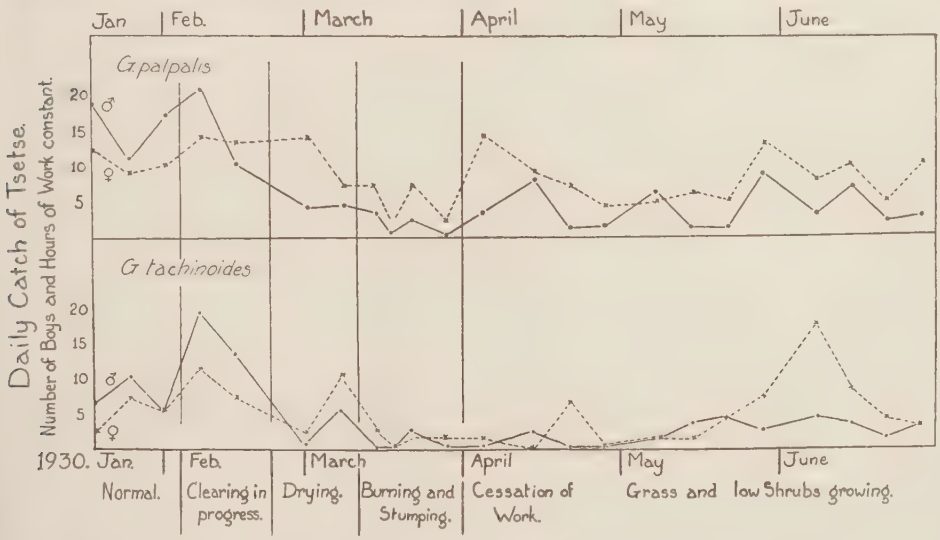


Fig. 7. Effect of clearing *Ficus congensis* association on *Glossina* at Makongo, 1930.

* [The rise in the female percentage may have been caused by an abrupt reduction in the normal food supply due to the clearing—a result that has frequently been noted by other observers since it was experimentally demonstrated by Fiske.—Ed.]

The clearing of the *Ficus* bush along the river was not so successful in driving out tsetse, and although *G. tachinoides* was practically eliminated until the end of May, *G. palpalis* remained in the clearing in fluctuating numbers even during the burning of the cut wood. Fig. 7 shows graphically the effect of clearing this fly-belt on both species. Fig. 8 shows the incidence of these species along the uncleared river, down stream, during the same period.

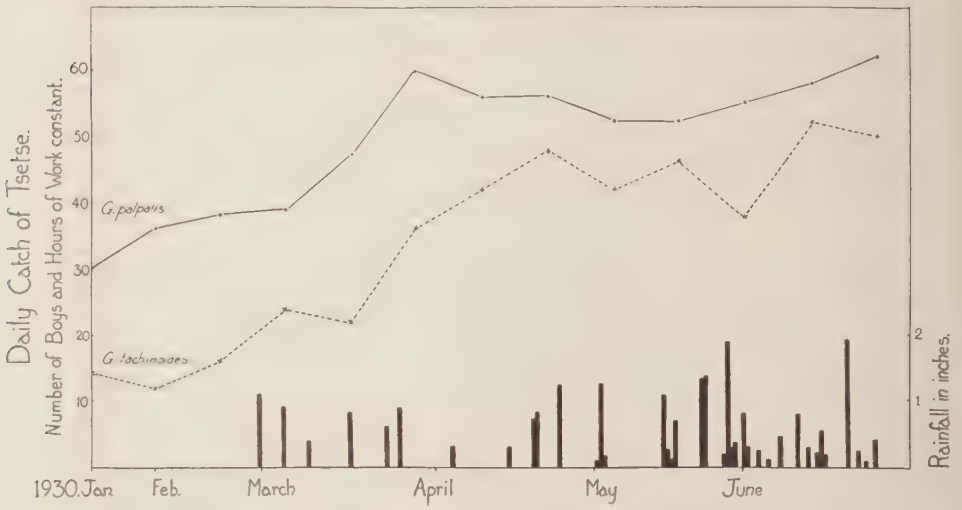


Fig. 8. Incidence of *Glossina* and rainfall on uncleared land at Makongo, 1930.

These riverside clearings enabled the making of some observations on the differential effect of clearing on the two species, *G. palpalis* and *G. tachinoides*. Previous to clearing, the proportion of *G. palpalis* to *G. tachinoides* was 3 : 1 in this fly-belt ; in April, after all work was finished, the proportion had increased to 5 : 1. At the same time along the uncleared river the proportion of *G. palpalis* to *G. tachinoides* was becoming less ; catches showed that this was due to a relatively greater increase of the latter species at this time of year, and the same thing was occurring on the Volta River at Yeji. Again, taking the female percentage for the two species caught in the clearing during April, *G. tachinoides* was showing a female percentage of 80 and *G. palpalis* only 64 ; on the uncleared river the figures were 44 and 41 respectively.

By June the river was very full and flooding its banks in places, driving the flies out of their original shelter under big stumps and clumps of re-growth close to the water's edge and causing them to shelter in a patch of thin bush outside the limits of the original clearing. This bush has since been cut. During May there was a very slight increase in the numbers of both species caught in the clearing, but during June there was a very marked increase in *G. tachinoides*. Along the uncleared river the two species were now being caught in approximately equal numbers and were showing a marked tendency to spread away from their primary foci. There was a definite up-stream migration of *G. tachinoides*, which would most probably account for the increase in this species in the clearings in June. The female percentage of catches in the clearing remained high, 68 for *G. palpalis* and 74 for *G. tachinoides*.

A marking experiment in which 565 tsetse were marked and liberated in the fly-belts immediately previous to clearing showed still further the more pronounced effect of clearing on *G. tachinoides* than on *G. palpalis*. Of the latter species 402 specimens were liberated, and 51 (12·7%) were recaptured in the same place, *i.e.*, in the clearings ; 45 (11%) were recaptured outside the clearings, catching extending to

over two miles up and down the river, and flies being recaptured in diminishing numbers up to this distance. The majority, however, were caught within a quarter of a mile of the end of the clearings. Two flies of this species were caught in the clearing 8 weeks after being marked and liberated.

Of *G. tachinoides* 163 marked flies were liberated and 9 (5·5%) recaptured in the clearings; 11 (6·8%) were recaptured elsewhere. One specimen was recaptured in the clearing after 8 weeks, but this was probably a re-introduction, as the only other recaptures in the clearings were 7 in the first week and 1 in the fourth week.

It will be seen then that, in the early months at least, the clearing was far more effective in driving out *G. tachinoides* than *G. palpalis*. It is possible that this is not a direct effect of the clearing at all, but due to a difference in preferred hosts of the two species. *G. palpalis*, feeding largely upon cattle and man, remained in the vicinity of the cattle road and town; *G. tachinoides*, preferring wild animals, followed them as they were driven away from the cleared areas.

Observations were discontinued from the end of June 1930 owing to the writer's absence on leave, but Makongo was again visited in December 1930. Re-clearing had already started under the supervision of the Medical Officer of Salaga, and the whole of the riverside clearings had been re-cleared and stumps were being dug up and burned.

In the *Isoberlinia* clearings north, west and south of Makongo there was a very dense re-growth of vegetation forming a low impenetrable bush not more than 5 or 6 feet high on the average. The most prominent feature of this was the tremendous growth of creepers that were covering everything and forming dense shrouds of matted vegetation over the stumps and bushes that remained in the clearings. This growth consisted mainly of four species: two creepers, *Paullinia pinnata* and *Manniophytor africanum*, which had been present in the uncleared plant community; and two introductions, *Psophocarpus palustris*, a wild bean, and *Ipomaea involerata*, a convolvulus, both of which grow normally in open damp places. Besides these creepers there were clumps of saplings grown up from unburned stumps and roots.

It is interesting that in the clearings north and west of Makongo the dominant tree of the original bush, *Isoberlinia doka*, had made very little re-growth, but that the re-growth consisted mainly of some of the smaller species which had formed the under-storey of vegetation in the original plant community. The re-grown plants, in order of their abundance, were *Ouratea flava*, *Vitex cienkowskii*, *Raphia vinifera*, *Elaeis guineensis* and *Ficus capensis*; the last-named was formerly inconspicuous. This may have a most important significance, as it is possible that the original tall woodland with the dominant *Isoberlinia doka* may never re-establish itself upon this ground, but that a secondary bush may become permanent, consequent upon the drying up of the ground upon the initial clearing.

South of the town where the ground is more swampy *Isoberlinia doka* formed the most prominent re-growth. Such space as was not occupied with creepers and bushes was densely grown with tall grass.

Details as to the exact nature of the growth in the riverside clearings were unfortunately not available, as re-clearing had been in progress for three weeks before Makongo was visited. Apparently there was a dense low growth of vegetation similar to that in the other clearings.

Despite this profuse vegetation in the clearings north and west of Makongo and the fact that the water-hole situated in their midst was in constant use by the townspeople, not a single tsetse could be found here. In the part of the clearing south of Makongo in which re-growth remained no tsetse were found except at the remote end of the clearing close to the footpath, and here only 3 male and 2 female *G. palpalis* were caught. In the re-cleared areas not a single fly was caught, although men working there, villagers washing and drawing water, and large herds of cattle passing

almost daily, offered an abundant and attractive source of food to tsetse. From quite reliable information tsetse were not numerous in these clearings before its re-growth was cut, except at the village water-holes where a few flies were always present.

Along the uncleared river at this time tsetse were quite numerous. Employing three boys, a total of ten catching hours spent in uncleared fly-belts produced 117 flies (70 *G. palpalis* and 47 *G. tachinoides*), whereas 26½ catching hours spent in the various clearings yielded only the 5 specimens of *G. palpalis* mentioned. After these observations the conclusion reached is that this dense re-growth of vegetation is definitely inimical to tsetse; not only are they not inclined to live in it, but apparently it acts as a barrier to their passage.

Summary.

1. Primary fly-belts round Makongo consisted of three different vegetational communities: a *Cynometra-Vitex* association along the main length of the Makongo river, on a clay soil; a *Ficus congensis* association along the river close to the town, on a sandy soil; and *Isoberlinia doka* woodland on moist sandy soil north-west and south of Makongo.

2. Secondary fly-belts of less dense vegetation occur in the orchard bush savannah round Makongo, and these are not colonised until the commencement of the rainy season.

3. *Glossina tachinoides* and *G. palpalis* both occurred in the riverside communities, and *G. palpalis* alone in the *Isoberlinia* woodland.

4. Along the river *G. palpalis* outnumbered *G. tachinoides* by 3 : 1 in the dry season. At the commencement of the rains *G. tachinoides* increased more quickly than *G. palpalis*, bringing their numbers very nearly equal, but at the end of the rains there was a decrease in *G. tachinoides* which restored the original proportion.

5. *G. morsitans* had been found at Makongo formerly but was not met with at the time of this investigation, its absence being due to the disappearance of the larger antelope from the neighbourhood.

6. Smaller game animals, small mammals and reptiles afforded an adequate food supply for tsetse in the fly-belts, and also passing herds of cattle, as well as natives from the village and travellers.

7. The distribution of *G. palpalis* within the fly-belts was markedly influenced by the proximity of a cattle road along which herds of cattle passed almost daily, and by village water-holes.

8. During the dry season the primary foci were always found to be the places of greatest relative humidity, and the fly does not tend to move out of these until the general atmospheric humidity has reached a certain fairly high degree.

9. In clearing the fly-belts the removal of all primary foci within a quarter of a mile of the town and of thick bush within 100 yards of water-holes was undertaken. The work lasted from the beginning of February to the end of March 1931.

10. The effect of clearing the *Isoberlinia doka* woodland was to banish *G. palpalis* completely, and it never returned to these clearings.

11. On clearing the riverside *Ficus congensis* fly-belt, *G. tachinoides* was practically eliminated for the first three months, but reappeared in the clearings in June when there was a general increase and up-stream migration of this fly. *G. palpalis* remained in this clearing in fluctuating numbers up to June, when observations were suspended.

12. 565 marked tsetse were liberated in the fly-belts immediately previous to clearing. Of *G. palpalis* 12·7% were recaptured in the clearings and 11% outside the clearings. Of *G. tachinoides* 5·5% were recaptured in the clearings and 6·8% outside.

13. Nine months after clearing (December 1930), a very dense re-growth of vegetation was found in the *Isoberlinia* clearings, but no tsetse could be found living in or passing through it. In the riverside clearings this re-growth had been cut and burned and no tsetse were found.

14. In the *Isoberlinia* clearings north and west of Makongo the original dominant *Isoberlinia doka* had made little re-growth, but the lesser shrubs and trees were the most conspicuous. South of the town on more swampy ground *Isoberlinia doka* formed the most prominent re-growth. A profuse growth of creepers covered the stumps and bushes giving the re-grown vegetation its dense and impenetrable character.

Conclusions.

The observations on the Makongo clearings are as yet insufficient for a full appreciation to be made of the success of the clearings. From the facts here detailed it seems that the small amount of clearing undertaken will effect a very satisfactory control of tsetse in the dry season at least. The only wet season observations were made during the few months immediately following clearing, and as has been found in previous clearing experiments, this is very little guide as to what will happen in subsequent years.

Apart from this effect of clearing on tsetse there are two points of considerable interest which have arisen during the course of the experiment. These are :—

(*a*) The possibility of making vegetational barriers against *G. palpalis* and *G. tachinoides*. If such a re-growth as resulted at Makongo could be maintained at either end of a riverside clearing it is possible that it would be an effective barrier against invasion of tsetse from the uncleared fly-belt into the cleared area.

(*b*) The possibility of permanently removing a primary focus of tsetse by alteration of the plant community by clearing. Such an effect could probably be produced only on one type of vegetation, a woodland vegetation on moist ground ; draining the ground would be a material aid.

The writer wishes to express his thanks to the Officers of the Political Department who undertook the work of clearing and also his indebtedness to Dr. P. Oakley for his invaluable help in organising the work and for the keen interest he showed throughout the experiment.

Explanation of Plate XLII.

Fig. 1. The Nasia River at Suguri. Incompletely burned stumps in the clearing showing dense re-growth of foliage four weeks after burning. *G. tachinoides* was invariably found sheltering in such clumps of re-growth. May 1929.

Fig. 2. The Nasia River at Suguri. The same as fig. 1 but two years after clearing showing tree stumps which had been completely killed by flooding after the first burning. There had been no farming or re-clearing, and the freedom of the river banks from vegetation is entirely due to flooding. No testse were found. January 1931.

Fig. 3. The Nasia River at Suguri. The Western limit of the clearing, showing the dense narrow band of *Cynometra vogelii-Vitex cienkowskii* association forming an archway over the river. Taken just after clearing. April 1929.

Fig. 4. The Tanne River Clearing. Bushes of *Mimosa asperata* growing in the clearing close to the water's edge. This plant was introduced into the clearing from higher up the river by its water-borne seeds, and the growth was sufficient to harbour numbers of *G. tachinoides*. Taken 14 months after clearing. May 1930.



Fig. 2.



Fig. 4.



Fig. 1.



Fig. 3.

Explanation of Plate XLIII.

Fig. 1. The Nagbo Clearing. Tobacco and maize growing in the cleared area. The banks of the stream have been kept free from vegetation. No tsetse were found in this clearing at this time. Taken 2 years after clearing. January 1931.

Fig. 2. Makongo. A village water hole in the midst of the dense *Ficus congensis* fly-belt. January 1930.

Fig. 3. Makongo. The same stretch of river as in fig. 2. Taken in January 1931, one year after clearing, and after the re-growth had just been cut. In the background can be seen the dense *Cynometra vogelii-Vitex cienkowskii* vegetation of the uncleared river banks.



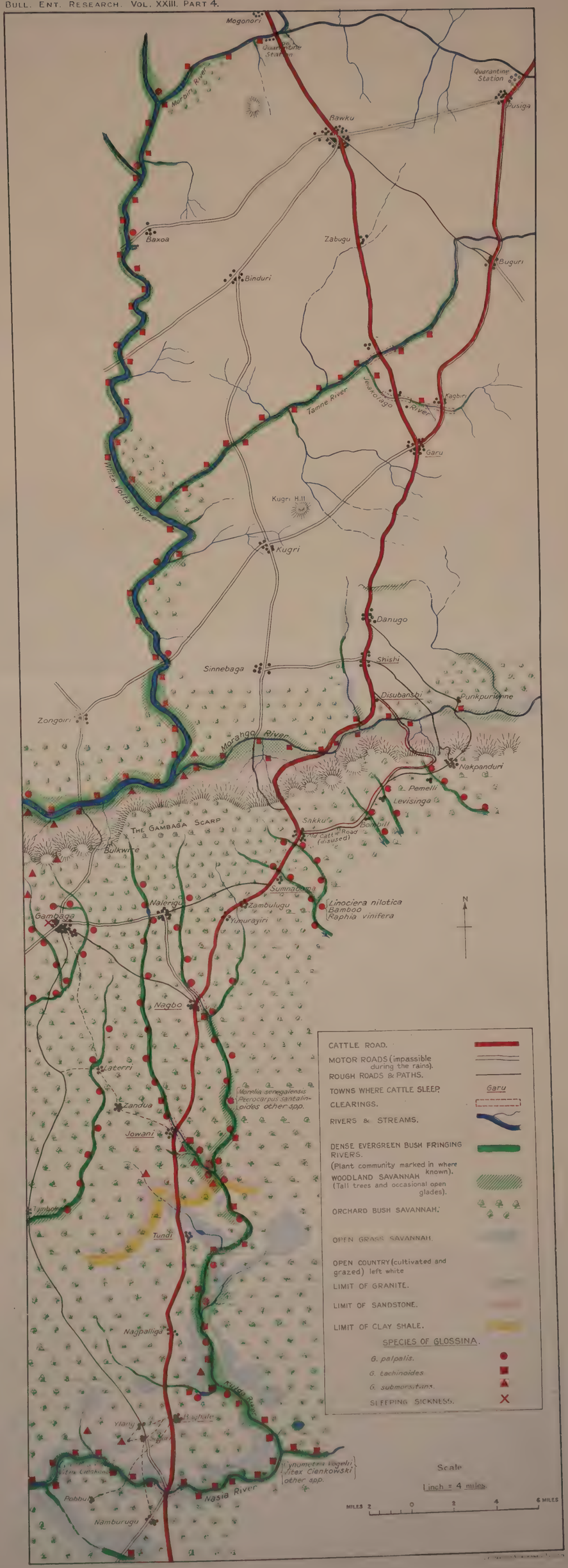
Fig. 1.



Fig. 2.



Fig. 3.


Magonori
Quarantine Station
Quarantine Station
Pusiga
Mordiri River
Bawku
Baxoa
Zabugu
Buguri
Binduri
Tamne River
Jaaxotago River
Kagbin
Garu
White Volta River
Kugri Hill
Kugri
Danugo
Sinnebaga
Shishi
Disubanshi
Punkpurienne
Zongoiri
Morango River
Nakpanduri
Pemelli
Levisinga
Sakku
Old Cattle Road (disused)
Bompill
THE GAMBAGA SCARP
Bulkwine
Sumnaboma
Nalerigu
Zambulugu
Yunurayiri
Gambaga
Linociera nilotica
Bamboo
Raphia vinifera
N
Nagbo
Laterri
Morelia senegalensis
Pterocarpus Santalinoides other spp.
Zandua
Jowani
Tundi
Nagpalliga
Kulpa River
Ylang
Bunhale
Pobbur
Nasia River
Namburugu
Tynanthera Vogelii
Vitex Cienkowski
other spp.
CATTLE ROAD.
MOTOR ROADS (impassible during the rains).
ROUGH ROADS & PATHS.
TOWNS WHERE CATTLE SLEEP.
Garu
CLEARINGS.
RIVERS & STREAMS.
DENSE EVERGREEN BUSH FRINGING RIVERS.
(Plant community marked in where known).
WOODLAND SAVANNAH (Tall trees and occasional open glades).
ORCHARD BUSH SAVANNAH.
OPEN GRASS SAVANNAH.
OPEN COUNTRY (cultivated and grazed) left white
LIMIT OF GRANITE.
LIMIT OF SANDSTONE.
LIMIT OF CLAY SHALE.
SPECIES OF GLOSSINA.
G. palpalis.
G. tachinoides
G. submorsitans.
SLEEPING SICKNESS.
Scale
1 inch = 4 miles.
MILES 2 0 2 4 6 MILES

ECOLOGICAL STUDIES ON APHIDES INFESTING THE POTATO CROP.

By W. Maldwyn Davies, B.Sc., Ph.D.,
University College of North Wales, Bangor.

Contents.

	Page
1. Introduction	535
2. Description of observational centre	535
3. On the nature of the initial infestation	536
4. The general infestation	537
5. Relative infestation by the different species	539
6. Intensity of the populations of aphides in a potato crop	540
7. Movement of aphides within the potato crop	541
8. Observations on the nature of colonisation and succession of the species ...	545
9. Summary	547

Introduction.

It is apparent on reviewing entomological literature that there is a real need for critical *field* studies on the aphides infesting the potato crop. This need has been emphasised recently owing to the role of aphides as vectors of virus diseases, since, clearly, the relationship between these aphides and their environment will have a direct bearing upon the degrees of transmission occurring in the field. The more common British species of aphides infesting potatoes are *Myzus persicae*, Sulz., *Macrosiphum gei*, Koch, and, to a lesser extent, *Myzus pseudosolani*, Theo. In addition, Theobald[1] includes *Aphis solanina*, Pass., and *Geoica (Tychea) phaseoli*, Pass., among the species attacking potatoes, and the writer has taken small numbers of the glasshouse species, *Myzus circumflexus*, Buckt., on potatoes in the field at three centres during 1931. Preliminary field observations on the potato aphides were made in connection with the scheme for the production of Welsh seed potatoes, and the results of these, in so far as they concerned that scheme, have been published jointly elsewhere.[2] It was apparent, however, that a more intense study of the biology and ecology of the insects was needed, and the existence of special seed potato centres in North Wales, with its very varied ecological conditions, and where an independent record of the incidence of virus diseases in the crops is being made, rendered this province particularly suitable for these studies.

The present paper is confined in the main to the investigation made at one centre during 1931 and is published at this stage to present salient points which have arisen and which are confirmed by previous observations. In addition, the technique developed for studies of this nature is presented.

Description of the Observational Centre.

The centre chosen for these observations was the College Farm, Aber, where it was possible to make weekly or, if necessary, daily observations. Further, at this centre the incidence of virus disease has been recorded by the writer's colleague, Dr. Whitehead, since 1921, and it is evident[3] that this centre is in a district where the spread of virus diseases is considerable. The potato field concerned is situated on a narrow stretch

of land (about one mile in width) lying between the mountains and the Menai Straits; it is flat, practically at sea-level, and the soil is a light stony clay. The field is bordered on the north-east by the Menai Straits; on the east by a small wood and a stream; on the south by the embankment of the London Midland & Scottish Railway, and beyond by fields leading up to the village of Aber with its several small gardens, and ultimately sloping to the mountains; on the west it is flanked by the majority of the lowland (some 200 acres) of the College Farm. The rows of potatoes ran from east to west; the potatoes were planted on 27th March and were first seen above ground on 15th May. Several varieties were grown in the field, but the observations were made on Sharpes' Express, Great Scot and Kerr's Pink.

Full details of the meteorological conditions during the observations are published under district 7b of the Monthly Crop Weather Report issued by the Ministry of Agriculture. Some indication of these conditions can be had from Table I, and comments relevant to the observations are as follows:—

May.—Fine at first; very unsettled later, heavy showers, sunny intervals. Temperature low; wind variable, easterly in latter part of month.

June.—Very unsettled, with heavy showers, thunder; last 3 days alone fine. Winds moderate in force, mainly N.W. to S.W. Temperature low.

July.—Showery conditions, temperatures low, sunny intervals. Winds moderate, mainly S.W.

August.—First and last weeks were very fine and sunny, winds light. Remainder unsettled, heavy thunder showers, stormy at times. Winds moderate, mainly N.W. to S.W.

September.—First week wet with heavy rain. Very fine weather followed with light winds, mainly N.W.

TABLE I.

Meteorological Records during Period of Observations.

Month	Temperatures (F.)		Rainfall inches	Sunshine hours	Wind
	Mean Max.	Mean Min.			
May	64	47	1·93	5·3	Mainly S.W., moderate
June	64	51	3·19	5·1	S.W. to N.W. ,,
July	64	54	2·21	4·0	Mainly S.W. ,,
August ...	59	53	4·85	4·5	S.W. to N.W., strong at times
September ...	59	48	3·52	4·4	Mainly N.W., moderate

On the Nature of the initial Infestation.

Periodical examinations revealed no aphides until 1st June, when 200 plants examined yielded two apterous viviparous ♀♀ *Myzus persicae* and one alate ♀ *Macrosiphum gei*, which were taken on three widely separate plants. This was the first record of aphides on potatoes in the field in North Wales in 1931. In a sheltered garden near Aber, however, two solitary apterous ♀♀ *Macrosiphum gei* were taken on widely separated plants on 18th May and one alate *Myzus persicae* was taken on 21st May. *Macrosiphum gei* were common on roses in the district on 1st May, and *Myzus persicae* were abundant on nectarine out-doors on that date, but no alatae were found in the colonies.

The great majority of the aphides first observed on potatoes both in gardens and in the field were *solitary apterous*, viviparous females. This fact required some explanation for the apterous nymphs were commonly taken at considerable distances

from all possible recognized winter food-plants. In the first place, the possibility of aphides having hibernated on weeds or various field plants was investigated, and data which uphold this view have been collected ; this will require confirmation during another winter. Secondly, it appeared possible that the few alatae (migrantes) which had appeared had deposited single nymphs and had migrated immediately after parturition. Evidence supporting this was forthcoming when early in June three separate instances were noted in which *Myzus persicae*, in the absence of any disturbing factor, immediately took to the wing after depositing a single nymph. Later in the season, of course, it was possible to find alate forms accompanied by a few nymphs. Again, the surprising absence of any quantity of alate aphides on the potatoes in the field prior to the initial infestation made it desirable to test the possibility of sprout infestation, prior to planting, as a source of initial infestation. Twenty-five seed potatoes, moderately infested with *Myzus persicae* (about 25 aphides per tuber), were planted in the normal way in the College garden on 22nd May. Each was isolated, prior to the appearance of the plants above ground, by placing a lamp-glass covered above with muslin on the soil above the tubers. These were not placed on immediately after planting, lest abnormal environmental conditions were produced. When examined on 6th June, 12 out of the 25 plants had apterous females of *Myzus persicae* present ; in no case, however, were there more than 5 aphides present, while single individuals were taken on six plants. This sufficed to show that aphides infesting sprouts prior to planting can be the cause of initial infestation. Walton[4] states that " planting kills the aphides and only in one instance was a single aphis found on a plant grown from an infested tuber, although forty such were examined." These experiments were made in May 1923, and meteorological records show that there was a much heavier rainfall and lower temperatures at this period than was the case in the present observations ; it is suggested that this may have accounted for the death of the aphides in the planted tubers. Three instances were observed this year which strongly suggest that initial infestation through infested seed had occurred in the field. At one centre the plants shortly after appearance above ground proved to be slightly infested with apterous *Macrosiphum gei*. An examination of the unplanted seed in the seed-box room showed that the sprouts were heavily infested with the same species. At another centre apterous *Myzus persicae* alone could be found on the young potato plants in the field, whereas in this case this species was the only one on sprouts in the seed-box room. Despite careful search in each case no alate forms could be found. The third instance appears more conclusive, at this centre the seed was sprouted in a glasshouse where *Myzus circumflexus* heavily infested the tubers—this Aphid is a glasshouse species rarely taken on potatoes outdoors. When the potatoes appeared above ground, at some distance from the glasshouses, apterous individuals of this species were found on the young growths. Again no alate forms were found either on the plants or in the glasshouse. This evidence, in conjunction with the observations on planted infested seed, shows that infested sprouts must be regarded as a possible source of initial infestation.

The general Infestation.

Previous work[2] has shown that comparative estimates of the degree of infestation of potato plants with aphides can most satisfactorily be made if the single leaf is regarded as the unit upon which counts are taken. The nature of the general infestation throughout the season was obtained, therefore, by examining periodically 100 leaves, taken at random, from varying positions on the plants as the crop was traversed once up and down. The number and species of aphides observed on each of the two sets of 50 leaves was noted, and if the leaf infestation on each 50 leaves varied more than 5 a further 100 leaves were examined and the average taken. The aphides are found normally on the lower surfaces of the leaves and are more or less evenly distributed between the upper and lower leaves. No significant difference between the infestation on the three different varieties was observed. The results of

the observations throughout season 1931 at the College Farm, Aber, are given in Table II. Comparative estimates of the aphis infestation at successful and unsuccessful seed potato producing farms have been published in a previous paper.[2]

TABLE II.

Infestation of Potato Aphides at Aber, 1931.

Date	% Infestation		Number of aphides per 100 leaves				Average no. of aphides per leaf
	Plant	Leaf	*M. gei*	*M. persicae*	*M. pseudo-solani*	Total aphides	
May 15* ...	nil	nil	nil	nil	nil	nil	nil
,, 27* ...	nil	nil	nil	nil	nil	nil	nil
June 1* ...	1·5	1·5	1 al.	2 apt.	nil	3	0·03
June 22 ...	25	9	9 apt.	4 apt.	nil	13	0·13
July 10 ...	72	31	74 apt.	20 apt.	nil	94	0·94
July 23 ...	100	86	215 apt. 1 al.	61 apt.	nil	281	2·81
Aug. 7 ...	100	53	78 apt. 1 al.	67 apt. 3 al.	1 apt.	148	1·48
Aug. 14 ...	100	38	50 apt. 1 al.	40 apt. 2 al.	4 apt.	97	0·97
Aug. 20 ...	75	15	6 apt.	23 apt.	2 apt.	31	0·31
Aug. 26 ...	(x)	22	9 apt. 1 al.	23 apt. 1 al.	2 apt.	36	0·36(x)
Sept. 15 ...	On this date all foliage had died						

*=200 leaves examined on these dates.

(x)=50% of the plants had lost foliage, counts made on remaining green leaves.

From Table II it will be seen that no aphides were found on potatoes in the field at this centre until 1st June. On 22nd June the leaf infestation had reached 9 per cent., and on 10th July it had increased to 31 per cent. When compared with previous years, this was by no means a heavy infestation, for at several centres 100 per cent. leaf infestation was recorded each year from 1928–1930 and as high an average as 34 aphides per leaf was observed. It is of interest to note, nevertheless, that the period of maximum infestation coincided with that occurring at other centres in the east of North Wales during 1931 and also during the seasons 1928–1930. A delay in the period of maximum infestation at certain western farms in S. Carnarvonshire has been referred to in a previous paper.[2] During August there was a decline in the degree of attack, which had fallen to 15 per cent. leaf infestation on 20th August. Subsequent to that date the leaves began to die down rapidly, so that on 26th August 50 per cent. of the plants were devoid of green leaves. Under these conditions the aphides moved to the green foliage, but the leaf infestation, despite a smaller area for feeding, only rose to 22 per cent. and the total aphides on a 100 random leaves was 36. By 15th September practically all the foliage was dead. Although in this case the death of the food-plant appeared to account for the disappearance of aphides from potatoes in the field, it was evident from examination at other centres where the foliage did not die down so soon, that the infestation under field conditions had reached negligible proportions by the

middle of September. Even in a sheltered garden near Aber where the leaf infestation had reached 100 per cent. in mid-July, there had been a reduction to 5 per cent. leaf infestation by 1st October, and *Myzus persicae* was the only species that remained.

It is significant that comparatively few alate aphides were present throughout the season, for never did they attain more than 3 per cent. of the total number of aphides. The small proportion of alatae may be accounted for by the moderate infestation, abundance of food, average temperature above 60 F. and over 15 hours daylight. Alate dispersal forms are not produced in large numbers under such conditions (Davidson,[5] Shull,[6] Wadley[7]). In instances of severe infestation in the field, however, no great increase in the proportion of alate forms has been noted, and it is evident, so far as transmission of virus diseases within the crop is concerned, that the apterae will play the more important part. During the last week in August it was observed that about 50 per cent. of the apterae possessed wing-pads, and it was clear that a winged generation was being produced. The factors influencing the production of alate forms are light, temperature, overcrowding and nutrition.[5, 6, 7] During the last week in August there was an average of 14 hours daylight and the average daily temperatures were max. 64°, min. 51 F.; such conditions with the absence of overcrowding would appear to rule out these factors as causing the production of alatae in the present instance. At this period, however, the foliage of the potatoes was rapidly dying down, and from the nature of the leaves it was evident that the nutrition value of the food-plant had changed. Doubtless this had produced a starvation effect, which according to Shull and Wadley quickly causes aphides to produce winged offspring. The plants, however, died down rapidly before matured alatae were produced.

Relative Infestation by the different Species.

The general infestation by the different species warrants further consideration. One factor which played an important part in the relative infestation was the degree of attack on the flower-heads of the potatoes. Flower-heads of the varieties Great Scot and Kerr's Pink began to make their appearance during the last week or so in June, and an examination on 7th July showed that 74 per cent. of the flowers examined were infested by aphides. It was obvious that *Macrosiphum gei* was the species which preferred this site, for 73 per cent. of the flower-heads were infested by this species, with an average of 5 apterous females to a flower head. Two alate *M. gei* were taken on 100 flower-heads on 7th July, but no alate *Myzus persicae* were found. Doubtless, the sudden rise in the leaf infestation by *Macrosiphum gei* witnessed between 10th and 23rd July is partly explained by the fact that on the latter date the majority of the flower-buds on these varieties had fallen and the aphides had moved to the leaves. Nevertheless, it was evident that the curve of infestation by *M. gei* rapidly attains its maximum towards the middle of July and declines with equal rapidity, so that on 20th August, when all the foliage still remained, only 6 apterous ♀♀ *M. gei* were taken on 200 leaves.

The flower-heads were not free from *Myzus persicae* but only 3 per cent. were infested with a total of 7 apterous ♀♀ on a 100 flower-heads. *Myzus persicae* appeared on the potato crop in small numbers at the same time as *Macrosiphum gei*, but the increase was more gradual and the maximum numbers attained by the latter species were never reached. *Myzus persicae*, however, maintained its infestation for a longer period, and on 20th August, when the numbers of *Macrosiphum gei* had declined, it outnumbered the latter species. This tendency for the curve of infestation of *Myzus persicae* to be less acute than that of *Macrosiphum gei* has been apparent at other centres not only this season but in the three previous years. In addition, the lag in the ultimate decline of the infestation by *M. persicae* has been evident, for this species predominated during late August and September on potatoes in North Wales; this fact will be discussed later. This year in a sheltered

garden near Aber on 2nd October, 5 per cent. of the potato leaves were infested with *M. persicae* possessing well developed wing-buds ; no aphides were found on these plants on 10th October.

Myzus pseudosolani was not observed in the field at Aber until 7th August and subsequently was present only in small numbers—less than 4 per cent. of the total aphides.

Intensity of the Population of Aphides in a Potato Crop.

An attempt to estimate the intensity of insect population is always made with reluctance because of the varied associated factors. It is felt, however, that some indication of the numbers of aphides present in an acre of potatoes is helpful both in apprehending the problems in ecology of these insects and also in understanding the role played by them as vectors of virus diseases. The chief numerical factor in the estimation is the number of potato leaves to an acre. The tubers were planted 15 inches apart, in drills 27 inches apart ; the average number of stems to a plant

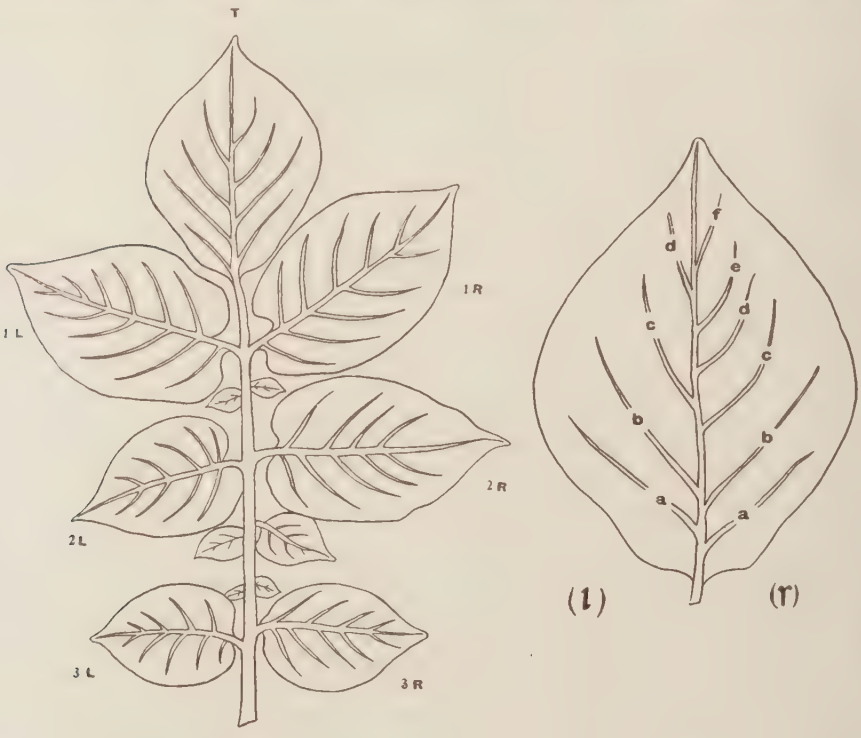


Fig. 1. Diagram of potato leaf showing divisions used in mapping the situations of aphides during observations.

was 6, and there was an average of 10 leaves to a stem during the period of maximum infestation. On this basis it is estimated that there would be 930,000 leaves to an acre. At Aber, in 1931, with 86 per cent. of the leaves infested and with an average number of 2·8 aphides to a leaf, the approximate number of aphides in an acre of potatoes is estimated at 2,000,000. It has been stated that the infestation was only moderate in intensity this year as compared with 1929 and 1930. In these years the maximum infestation during mid-July attained 100 per cent. leaf

infestation and an average number of above 30 aphides to a leaf at several centres. In such cases it is estimated that the infestation would be above 27,000,000 aphides in an acre of potatoes.

Movement of Aphides within the Potato Crop,

Critical observations were made to ascertain the degree of movement of aphides in the crop of potatoes, for apart from its ecological interest it is obvious that the degree of movement is a salient factor in the role of aphides as vectors of disease. The factors influencing movement are subjects of continued study.

TABLE III.

Section of Records on the Movement of Potato Aphides.

Row 100 ; N.W. situation. Variety, Great Scot.

Leaf	6th July	10th July	17th July	23rd July
15	0	2L f-g(l), 1p, 2pn.	1R a-b(r), 2gn.	T. c-d(l), 1gn. 3L a-b(r), 2p.
16	0	0	2L c-d(l), 2g. T a-b(r), 2p. 2R b-c(r), 1gn.	1R e-f(l), 1p.
17	0	T a-b(l), 1g. 3L a-b(r), 1p.	3R d-e(l), 1pn. 1L a-b(r), 2g.	3L a-b(r), 1g. 1R e-f(l), 1p. 2R c-d(r), 2gn. 3R a-b(l), 1p.
18	0	1R c(r), 1p. 2L c-d(l), 1gn.	0	T. e-f(l), 2g. 2L, d-e(r), 1g, 1gn. 1R. d-e(r), 1p, 1g.
19	0	T. d-e(l), 1g.	3L. g-h(r), gn. 1R d-e(l), 1g. 3R. a-b(r), 1g.	1L. e-f(r), 1g, 1pn.
20	0	1L. a-b(r), 1g.	T. c-d(r), 1p, 1pn.	1L. a-b(l), 1g. 4L. c-d(r), 1gn. 1R. f-g(l), 1g. 2R. d-e(r), 2p. 3R, d-e(l), 1g, 1pn.

Some methods of marking observed aphides were necessary if the observations were to be reliable. Spraying aphides with coloured stains was tried and proved practicable for certain studies of short duration. Apart from the fact that, save in alate forms, such stains were removed on moulting, it was clear that the action of spraying, or of feeding upon coloured fluids, would be factors which themselves would influence movement. Hence it was desirable to develop a technique which would not introduce a factor which would stimulate movement. For this purpose critical mapping was resorted to. On 15th May, prior to the initial infestation, 100 single leaves in 5 groups of 20 consecutive plants at different parts of the field were marked by tape. Each plant was numbered by a label in the soil at the base, so that it was certain that the same leaves were being observed throughout the season. It was not sufficient, however, to note the number of aphides on a leaf at each observation, for a variation in numbers would not necessarily mean that the movement had been in proportion to that variation. Obviously more detailed mapping was required, and for this purpose the leaf was viewed as subdivisions shown in fig. 1. Each leaf was divided into leaflets (*a*) and each leaflet mapped according to the nervures (*b*). In this way a record 52·2L b–c(r), 1p. would mean that

one apterous specimen of *Myzus persicae* was observed on the taped leaf on plant 52, on the second leaflet on the left and between the second and third veins on the right side. In the case of the few alate forms (al) would be added, while in the case of nymphs, the index used was (gn) or (pn) for nymphs of *gei* and *persicae* respectively. Although from the description of this method it may appear cumbersome it was particularly efficient in practice, for it was soon possible at the first glance at the Aphid on the leaf to interpret the position in terms of the formula. By this method it was possible to mark the site of the particular aphides without any disturbance in their normal environment. The identification of the different species without removal from the leaf was not so formidable as at first anticipated. After a series of test identifications on aphides in the field which were later removed to the laboratory for confirmation, it proved possible to identify even the nymphs of the species *Macrosiphum gei*, *Myzus persicae*, and *Myzus pseudolani*, with a high degree of accuracy. The aphides were identified by the combined characteristics of general contour, colour, length of antennae, shape of cornicles, etc. The type of information obtained by these records is seen in Table III, which gives only a section of the records.

Weekly Observations on the Movement of Aphides.

Observations involving the use of the method described were made at weekly intervals throughout the season. Single leaves on a 100 separate potato plants were taped. The observational leaves were arranged in five groups widely separated throughout the field. Each group consisted of 20 taped leaves—one such leaf on 20 adjacent plants in the same row. At each visit a record of the position of the aphis population was taken by means of the formula described, and the records were filed. These records for the entire season provide data concerning both movement and succession of the insects. Movement was revealed under two headings. Firstly, *movement of site* was demonstrated and a movement of site of $\frac{1}{2}$ inch, that is, across leaf-veins on the same half, or to the opposite half of the leaflet, would be recorded by this method. Secondly, *movement to or from the leaf* was shown by the records. In this case, however, such instances as the movement of an adult aphis from the leaf and simultaneously the movement of an aphis of the same age and species to that particular leaf would be recorded as " uncertain movement." Thus the movement to or from a leaf under this category will be the minimum amount of such movement, since instances included under " uncertain leaf movement " might have been movement from leaf to leaf. It will be seen later that owing to the degree of movement that took place this point proved insignificant. Only the marking of the particular aphides, the objections to which have already been mentioned, would give more precise data and even then the interchange of marked aphides would be uncertain.

An important aspect, however, is the relationship between movement from leaf to leaf and that from plant to plant. During the period of maximum infestation, when the leaves of adjacent plants in the same row, and also those of plants in adjoining rows, touched and intermingled, the movement from leaf to leaf will be closely comparable to the movement from plant to plant. Again, definite marking of the aphides would be necessary to ascertain such movement. Hence on 8th July 300 apterous *Macrosiphum gei* and 200 apterous *Myzus persicae* were collected and sprayed, by means of a very fine atomiser, with a solution of aniline blue (including gum arabic). These aphides were liberated at 12 noon on a plant in the centre of a separate section of the field. Slight rain fell during the afternoon, followed by a strong wind which had abated when observations were being made the following day ; the weather conditions were somewhat typical of many days during the summer of 1931. Examination showed that only 4 coloured aphides (1 *gei* and 3 *persicae*) were found on the plant on which they had been liberated 24 hours previously. On adjoining plants in the same and adjacent rows not more than 3 or 4 marked

aphides were taken on a plant, while single sprayed aphides were taken on six separate plants 7 yards from the spot where they had been liberated. Four of these were taken to the north-west, in the direction of the wind prevailing at the time. Although the act of spraying of the aphides introduced an unnatural factor influencing the movement, the spray dried very quickly and there appeared no further interference with the normal habit. Hence, whereas such spraying cannot be used to ascertain the normal movement of aphides within the crop, it does provide some indication of the nature of movement *once the aphides are on the move*. It would thus appear that once on the move, the aphides can easily and readily move from plant to plant, and movement from leaf to leaf is an indication of the amount of movement from plant to plant.

The data concerning movement on the 100 observational leaves throughout the season at Aber are set out in Table IV. The movement of site is shown in columns 3 and 4. In column 5 the movement to and from the leaf is given and, as stated, includes only those instances where such movement was positive and hence is the minimum amount of movement from leaf to leaf. Column 6 includes those records where there was a possibility that the aphides observed might have been replaced simultaneously by other aphides of the same age and species, and hence movement from leaf to leaf becomes uncertain.

TABLE IV.

Weekly Observations on Movement of Potato Aphides.

Results compiled from weekly records of aphis population of 5 groups of 20 observational leaves.

Dates of observations	Numbers observed on 100 leaves		Average % of aphides							
			Remained stationary		Moved site		Definite movement to or from leaf		Uncertain movement from leaf	
	gei	*pers.*	*gei*	*pers.*	*gei*	*pers.*	*gei*	*pers.*	*gei*	*pers.*
May 15, 30, June 15, 20, 26	nil	nil	—	—	—	—	—	—	—	—
June 26 & July 10 ...	79	26	0	0	100	100	100	100	0	0
July 10 & July 17 ...	182	77	0	0	100	100	91	100	9	0
July 17 & July 23 ...	292	137	0	0	100	100	84	91	16	9
July 24 & July 31 ...	246	115	0	0	100	100	93	94	7	6
July 31 & Aug. 7 ...	163	89	0	0·6	100	99·4	90	94	10	6
Aug. 7 & Aug. 14 ...	120	59	0	1	100	99	93	98	7	2
Aug. 14 & Aug. 21 ...	51	41	0	0	100	100	100	100	0	0
Aug. 21 & Aug. 26 ...	7	25	0	0	100	100	100	100	0	0

It will be seen from Table IV that the 1,140 individuals of *Macrosiphum gei* and the 569 *Myzus persicae* (with the exception of two separate specimens on 7th and 14th August) had all moved their site after a weekly period. Even in the two exceptions it is possible that they were replaced by two similar specimens of *Myzus persicae* and hence a movement not recorded. For all practical purposes, therefore, it can be stated that within a week, at all periods of the season, every aphis had changed its feeding place. Column 5 gives the average percentage of aphides which

the records showed had definitely moved to or from the observational leaves. In these figures the presence of nymphs on the second date of observations is not included, for clearly their presence does not necessarily mean movement. Hence it is seen that, in addition to the appearance of nymphs, over 84 per cent. of the aphides of both species moved to or from the observational leaves within the weekly interval. Instances in which movement was probable but uncertain are given in column 6, and when it is realized that some, if not all, of these insects may have moved, it will be seen that there is practically constant movement of the aphis population within the potato crop. In view of these results it was desirable to ascertain the degree of daily movement.

Daily Movement.

Observations on the daily movement were made on two occasions: early in the season on 25th and 26th June, and again at the period of maximum infestation, 23rd and 24th July. The meteorological conditions during the first observations can be gleaned from the following records taken ¼ mile from the potato field :—

Temperatures: mean max. 64·5°F.; mean min. 44·5°F. Rainfall: trace. Wind: N.E. changed to S.W. General: Very fine, sunny, light breeze.

At this date, with only 9 per cent. leaf infestation and an average of 0·13 aphides to a leaf, difficulty was experienced in getting sufficient numbers of suitable leaves possessing aphides for observational purposes. Ultimately, 15 leaves on separate plants scattered throughout the field were taped. The total number of aphides mapped was 23, which although small was considered representative of the aphides present at that date. The results can be summarized as follows: 14 apterous *Macrosiphum gei* and 9 apterous *Myzus persicae* were mapped on the morning of 25th June; when observed 24 hours later it was seen that 7 *gei* were in the same situation, whereas the other 7 had moved off the leaves; 8 *persicae* remained stationary, while one had moved. These results point to very slight movement at this season of the year. It is of interest to note that in this case *Macrosiphum gei* were more active than *Myzus persicae*. More importance is attached to the records in mid-July when more aphides were present.

The meteorological conditions during the second observations on the daily movement can be gleaned from the following :—

Temperatures: mean max. 66°F.; mean min. 54·5°F. Rainfall, nil. Wind: S.W. Sunshine: 6–7 hours. General: Cloudy at first, warm and fine later.

On 23rd July 100 per cent. of the plants were infested and 86 per cent. of the leaves carried aphides, with an average number of 2·81 aphides to a leaf. The plants on this date were well grown and the leaves of adjacent plants, both in the row and in the next drill, touched. The records were made on the same 100 observational plants, and the results are summarised in Table V.

These and previous records show no appreciable difference in the degree of movement on the different varieties of potatoes, and this is supported by the data given in Table V, in which the results of daily movement are compiled. It is thus possible to group the varieties together and consider the averages. Dealing first with *Macrosiphum gei*, 241 individuals were observed on the 100 observational leaves; 16 per cent. of these were found to be in precisely the same site after an interval of 24 hours, whereas the remaining 84 per cent. had definitely changed their site of feeding. When the records are considered from the point of view of movement to or from the leaf, then 52 per cent. of those which had moved could definitely be stated to have moved to or from the observational leaves within the 24 hours. Although the remaining 32 per cent. had moved, it was uncertain whether or not they had moved to or from the observational leaves. In the case of *Myzus persicae* when 103 were

observed, 27 per cent. were found in the same site 24 hours after the first observation, whereas the remaining 73 per cent. had definitely changed their feeding site. Again 52 per cent. of those which had moved definitely left the leaf on which they had been feeding, but it was uncertain whether the remaining 21 per cent. of those which had moved had definitely moved from the leaf or whether other aphides of similar age and species had replaced those originally observed. It is evident, however, that a considerable percentage, at least 73 per cent., of the aphides had moved their feeding sites within 24 hours, and of these at least half had moved from the leaves upon which they had been feeding.

TABLE V.

Observations on the Daily Movement of Aphides.

Date: July 23, 24. Varieties: Great Scot, Kerr's Pink.

Row—Variety	Number of aphides observed		Percentage of aphides							
			Remained stationary		Moved situation		Moved to or from leaf*		Movement to or from leaf uncertain	
	gei	*pers.*	*gei*	*pers.*	*gei*	*pers.*	*gei*	*pers.*	*gei*	*pers.*
10 Kerr's Pink ...	40	20	15	30	85	70	45	40	40	30
60	46	14	26	22	74	78	57	64	17	14
70	55	15	13	27	87	73	47	73	40	0
40 Great Scot ...	31	21	16	20	84	80	71	43	13	37
100 ,, ...	69	33	10	36	90	64	38	39	52	25
Totals ...	241	103 Av. %	16	27	84	73	52	52	32	21

*Excluding nymphs.

It should be noted that the weather conditions during the daily observations were comparatively fine and warm with no rainfall and the wind light. The high mobility of the aphis population witnessed in the weekly records during periods of heavy rain and high wind might have been attributed to these factors, but the daily observations indicate that movement is also considerable under fine conditions. The results of both daily and weekly observations, therefore, demonstrate the very high degree of mobility that exists among the aphides infesting the potato crop.

The comparative degree of movement of aphides on potatoes at successful and unsuccessful seed potato producing farms has been studied but will be subject to further investigation.

Observations on the Nature of Colonisation and Succession of Aphides.

The formation of localised colonies, the personnel of which remains more or less stationary over a period of several weeks, is a common feature among aphides. The records obtained in the present observations give some indication as to the mode of infestation by potato aphides. Examination of the records for the entire season shows that in the case of *Myzus persicae* there was only one instance where individuals (not necessarily the same ones) of this species were found on the same leaf at each examination during four consecutive weeks, and two such cases were noted for *Macrosiphum gei*. Further, four instances of individuals of *Myzus persicae* being present on the same leaf at three consecutive weekly observations were

recorded, and 10 such cases were noted for *Macrosiphum gei*. Many instances are present in the records when 6–10 aphides of one species or the other were found on the observational leaf, yet no individuals of that species were present the following week. It was thus clear that no attempt to establish local colonies on the leaf of the food-plant was made under these conditions. It would seem that in the case of aphides infesting potatoes, where there is a wide surface area of food-plant, all equally favourable to attack, dispersion of nymphs and adults is of frequent occurrence, and hence only under special conditions are the colonies maintained intact.

An interesting case of the failure of migrating aphides to establish the species upon potatoes was observed at several centres throughout North Wales during the first week in June. During this period alate *Anuraphis padi*, Linn. (=*helichrysi*, Kalt.)—the leaf-curling plum aphis—migrated from plums to their summer food-plants. They were commonly found on potatoes, where from 1–8 alate specimens were taken on about 25 per cent. of the potatoes examined. It was at first thought that they had alighted temporarily, but observation showed that in practically all cases the aphis, which was usually within the folded leaves at the apex of the plant, had its rostrum inserted into the young leaves and was feeding. Such specimens were found to remain in the same position for several days and made no attempt to leave the plant. Careful examination revealed no nymphs of this species, though on such plants as *Myosotis* and *Chrysanthemum* well developed colonies could be found. Towards the end of June dead alate forms of *Anuraphis padi* were commonly found on potatoes near the site where they had been feeding. It would appear that, although able to feed upon the potato leaf, such feeding is not conducive to the production of offspring.

There was little indication of any definite succession in the establishment of the different species of aphides on the potato. *Macrosiphum gei* and *Myzus persicae* infested the leaves at the same time. The contrast in the nature of the curve of infestation has been mentioned. The extended infestation of *Myzus persicae* is, however, interesting and may prove important. This species was predominant on potatoes during the latter stage of growth of these plants, and it was observed, after all potato foliage had died down, that this species readily established itself on several plants other than the potato commonly found in the potato field. Such plants include swedes (*Brassica napus*), cabbages (*B. oleracea*), chickweed (*Stellaria media*), goosefoot (*Chenopodium album*); a complete list is being compiled. The extent of the establishment on swedes, for instance, is seen by the fact that in the present field 75 per cent. of the swedes occupying the remainder of the same field were infested with from 1 to 10 apterous *Myzus persicae* on 25th November. This fact is not only interesting from the point of view of hibernation of this species but may be significant in reference to the part played as vectors of leaf-roll. If, for instance, we assume that the normal mode of hibernation of *Myzus persicae* is in the egg stage on peach, nectarine, *Daphne* and other plants, then, in view of the consensus of opinion (Smith[8]) that the infective principle of plant viruses is not inherited by insects, it must be assumed that the majority of aphides in the spring are non-infected and will require a period during which to feed upon diseased plants before transmission can take place in the field. This would delay transmission in the field and at centres where movement was slight, particularly where the foliage dies down early, for the crop would mature before much transmission could take place. It is well known that under glass *Myzus persicae* will continue to reproduce parthenogenetically for many years, but in North Wales, at least, such a source of initial infected aphides would be extremely local. On the other hand, if these aphides overwinter as adults out-doors they cannot be overlooked as sources of initial infestation of leaf-roll. Further, in view of the prevalence of *Myzus persicae* on swedes and other plants in the root field which has grown a crop of potatoes moderately infested with leaf-roll alongside these plants, it would be of interest to ascertain the fate of the virus in these plants. Although the possibility of such plants acting

as symptomless carriers of the virus may appear remote, the position concerning the continuity of the disease in the field would be unsatisfactory unless such a point was examined. Dr. Whitehead is investigating this aspect.

There was no evidence that *Macrosiphum gei* established itself fully on such plants in the autumn, though it was found in small numbers on other plants in the summer.

Summary.

1. Ecological studies on aphides attacking potatoes were commenced in 1928 with a view to elucidating certain problems of entomological interest and also the role of these insects as vectors of disease. The species include, *Myzus persicae*, Sulz., *Macrosiphum gei*, Koch, and *Myzus pseudosolani*, Theo.
2. The present study is confined mainly to the infestation of aphides on potatoes at a selected centre which is described.
3. Solitary apterous viviparous females were in a majority on potatoes during the period of initial infestation in early June. Their presence is explained by (1) the overwintering of aphides on weeds and field plants, (2) the first few alatae depositing single nymphs and then migrating, (3) infection from infested seed.
4. The maximum infestation was reached during mid-July, when 86 per cent. of the leaves were infested and there was an average of 2·8 aphides to a leaf. The infestation was below that of the previous three years. *Macrosiphum gei* bred up rapidly, at first on the flower-heads, and was the predominant species, its decline in numbers being equally rapid. *Myzus persicae* increased more slowly and did not reach such numbers, but the maximum was maintained longer and the disappearance of the species was delayed. *Myzus pseudosolani* was only taken in August and then in small numbers.
5. An estimate of the intensity of the aphis population is attempted, and in the present moderate infestation of 2·8 aphides to a leaf it was of the order of 2,000,000 aphides to an acre of potatoes.
6. A technique was established to ascertain the movement of aphides within the crop. Weekly records on observational leaves revealed that 100 per cent. of the aphides moved their site and at least 84 per cent. of each species moved from leaf to leaf within the weekly period. Daily records during the period of maximum infestation showed that 84 per cent. of *Macrosiphum gei* and 73 per cent. of *Myzus persicae* changed site within 24 hours, and of these at least 50 per cent. moved from the leaves upon which they had been observed.
7. It was noted that no attempt was made to maintain large local colonies, for the movement of both adults and nymphs was frequent, and observed colonies soon dispersed. The extended infestation of *Myzus persicae* is discussed with reference to its establishment on field plants, other than potatoes, during the autumn and winter.

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SOME AUSTRALIAN SPECIES OF *CALLIPHORA* (SUBGENERA *NEOPOLLENIA* AND *PROEKON*).

By G. H. Hardy,

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While on a recent visit to Victoria and South Australia, I made an attempt to collect long series of Calliphoras belonging to the subgenera *Neopollenia* and *Proekon*; a special visit was made for this purpose to Seaford and to Western Port, Victoria, the type localities of *C. hilli*, Patton, and *C. rufipes*, Macquart, respectively. The collections made represent at least seven species of *Neopollenia* and two of *Proekon*.

Subgenus **Neopollenia.**

My studies in *Neopollenia* lead me to suggest that the species may be classed into definable groups on the structures of the male, but are difficult to distinguish on characters other than genitalia; nevertheless I have attempted to make a key that may be workable for the determination of females in the field. With the new species incorporated here, there are six groups recognisable, and there are at least two other groups known in collections, but insufficient material has yet been collected for their study.

The *C. stygia* group contains *stygia*, F., and *australis*, Boisd.

The *C. fulvicoxa* group contains but one known species, *fulvicoxa*, Hardy, which comes rather close to the next group.

The *C. rufipes* group possibly contains *hilli*, Patton, and certainly *fallax*, Hardy. I have a specimen of *C. rufipes*, Macq., determined by Patton, that agrees with my own determination of that species, but it remains to be seen whether there are any real differences between this specimen and *C. hilli*.

The *C. canimicans* group is now represented by three species: *canimicans*, Hardy, *tessellata*, Bezzi (*nec* Macquart), for which I now propose the new name *bezzii*, and *auriventris*, Malloch; the last was described from a female, but presumably belongs here.

The *C. sternalis* group contains two species, *C. deflexa*, sp. n., and *C. sternalis*, Mall. The group is remarkable for the large size of the hypopygium, which character is very noticeable even when the genital organs are retracted.

The *C. tibialis* group is almost certainly a complex. Two forms are regarded as being distinct and occur in Brisbane; they are under further observation. The typical form, with its black femora and brown or almost black tibiae, frequents the ground in and around rather dense scrub and hedges, whereas the other and more abundant form is to be taken sporting on the tops of the shrubs. Both may inhabit the same spot, but those taken on the tops of the shrubs are invariably the type with lighter coloured legs, the femora being brown or more or less stained with black. The two forms do not intergrade and therefore both sexes are readily picked out. Drawings made of their genitalia have not shown any marked distinction between these organs. The second form is not met with in the southern States, whereas the typical form is plentiful there.

Key to the Females of Neopollenia.

1. Three presutural acrostichals, or if only two, the eyes very widely separated ; legs yellow 2
   Only two presuturals ; frons about as wide as long 4
2. Eyes very wide apart, frons much broader than long (*stygia* group) ... 3
   Frons only about as broad as long ... ... *fulvicoxa*, Hardy
3. Pulverulence of frons golden ; East Australian species ... ... *stygia*, F.
   Pulverulence of frons silvery ; West Australian species ... *australis*, Boisd.
4. Scutellum normally with four marginal bristles ; legs entirely black ; body always with yellow hairs (*canimicans* group) 5
   Scutellum with only three marginal bristles ; legs never entirely black, the tibiae at most being deep brown 6
5. Abdomen with yellow hairs ... ... *canimicans*, Hardy ; *bezzii*, Hardy
   Abdomen without yellow hairs ... ... *auriventris*, Mall.
6. Body with yellow hairs ; femora always yellow (*rufipes* group) *rufipes*, Macq. ; *fallax*, Hardy
   Body entirely without yellow hairs ; femora black or at least partly stained with black (*tibialis* group) ... ... *tibialis*, Macq.

The females of two species are unknown, but judging from the characters of the male, these would run to couplet 6, and one, *C. deflexa*, may possibly be confused with *C. fallax*, but the other, *C. sternalis*, should be distinctive enough as it doubtless resembles the male in having the femora black or mainly so. I have made several attempts to discover the female of *C. deflexa* in collections of *C. fallax*, using the slight differences found in the males as a guide, but so far I have not succeeded in finding a specimen.

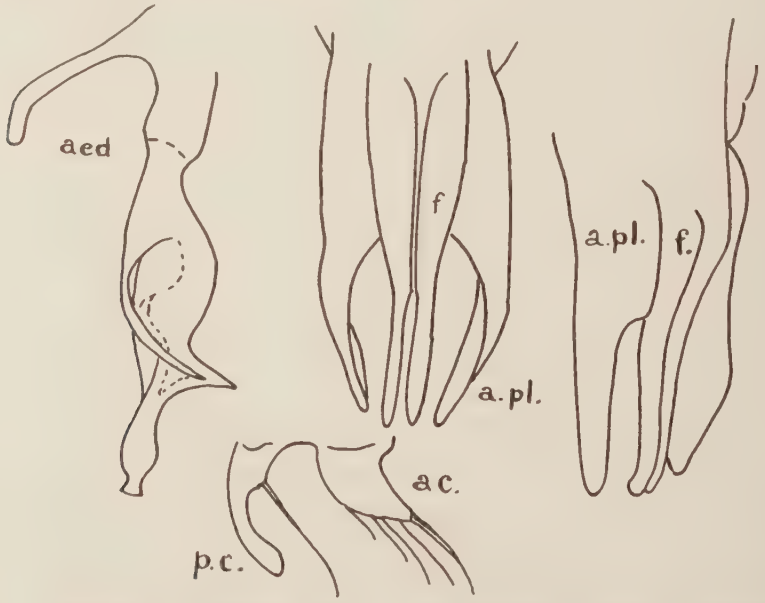


Fig. 1. Male genitalia of *Calliphora stygia*, F. : *aed*, aedeagus ; *f*, forceps ; *a.pl*, accessory plate ; *p.c*, posterior clasper ; *a.c*, anterior clasper.

Calliphora stygia (fig. 1).

Musca stygia, Fabricius, 1781.

Calliphora stygia (F.) Hardy, Bull. Ent. Res., xxi, 1931, p. 444 (which see for references and synonymy).

The male has the eyes contiguous, the upper facets being much enlarged. The frons of the female is excessively wide, the length in proportion to width being about 2 : 3. Normally three presutural acrostichal bristles are present, but they are sometimes reduced to only two pairs, and there are three pairs of marginals on the scutellum. Yellow hairs occur plentifully on this fly, being on the pleurae, venter and the dorsal area of the fourth tergite of the abdomen. The legs are yellow with the tarsi black. Unlike most species of *Neopollenia*, the strut of the aedeagus can be separated from the remainder of that organ for the greater part of its length, instead of being united by a membrane. The forceps and accessory plates are somewhat slender and long.

There are two variations of this species of which I have not yet been able to examine the genitalia. One of these has only two presutural acrostichal bristles ; the other is a much smaller form that at first sight appears distinctive, and gradations between it and the more normal form do not seem to occur.

Somewhere between Robe and Mt. Gambier, South Australia, I found this species in numbers far greater than I had experienced before, along some miles of bracken-covered paddocks, but I could discover no other species associated with it.

Calliphora australis, Boisd.

Musca australis, Boisduval, Voy. l'Astrobe, Ent. ii, 1835, p. 669.

Calliphora australis (Boisd.) Hardy, Bull. Ent. Res., xxi, 1930, pp. 442, 444.

Eyes of the male separated by about the width of the ocellar tubercle ; the frons of the female broader than long, about the proportion of 3 : 2. Three presutural acrostichals are present and three strong marginal scutellars ; in addition there is a weak marginal scutellar bristle nearer the base in all the specimens examined. Yellow hairs are plentiful on the pleurae, sides of the abdomen, venter and, in the female only, on the fourth abdominal tergite. The aedeagus conforms to that of *C. stygia*, having the same type of strut, but the portion that lies beyond the strut is conspicuously shorter, and in addition the aedeagus differs at the base. The forceps, accessory plate and the posterior clasper, are as in *C. stygia*.

WESTERN AUSTRALIA : Swan River, September (*W. Andrewartha*) ; three males and one female kindly supplied by Dr. I. M. Mackerras, who made the mount of the genitalia.

Calliphora fulvicoxa, Hardy.

C. fulvicoxa, Hardy, Bull. Ent. Res., xxi, 1930, p. 445.

SOUTH AUSTRALIA : Adelaide, i, 1931 ; 19 males and 28 females, mostly from the National Park.

Hitherto this species was only known from Queensland. It was not met with in Victoria.

Calliphora bezzii, sp. n. (fig. 2).

Calliphora tessellata, Bezzi (*nec* Macquart), Bull. Ent. Res., xvii, 1927, p. 45.

There can be little doubt concerning the identity of *C. tessellata*, Bezzi, as there is a long series before me from the type locality. Previously I suggested it might be identical with *C. canimicans*, but there is ample difference in the genitalia to permit its separation.

Eyes of the male separated to the width of three ocelli ; frons of the female about as long as broad, yellow, with a slight silvery sheen. On the thorax the pleural hairs are nearly all yellow and the bristles black. The scutellum has four

pairs of marginal bristles (rarely apparently three), which are often augmented by extra ones. All hairs of the abdomen on the upper side black, except on the fourth tergite, where many of the shorter hairs are yellow. On the underside of the abdomen all hairs yellow. Legs entirely black, with yellow hairs on the coxae and femora.

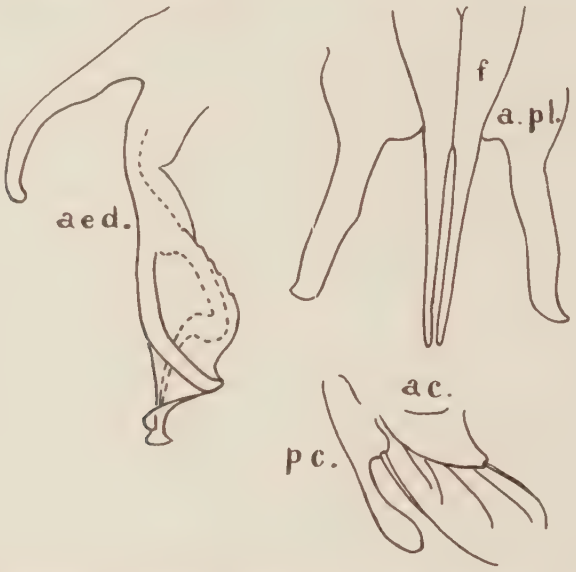


Fig. 2. Male genitalia of *Calliphora bezzii*, sp. n.: *aed*, aedeagus; *f*, forceps; *a.pl*, accessory plate; *p.c*, posterior clasper; *a.c*, anterior clasper.

The aedeagus (fig. 2) is very like that of *C. canimicans*, but the dark strut is conspicuously bent forwards and the anterior clasper is strongly developed. The shapes of the various parts differ, such as Lowne's spine, the forceps and the accessory plate. Seen laterally, the accessory plates curve strongly forward and end in a point, whereas those of *C. canimicans* curve gently and are rounded at the apex.

VICTORIA: Seaford, January and February, 25 males, 74 females.

This species has the head narrower than in *C. canimicans*, a character that is noticeable in both sexes but difficult to define.

Calliphora deflexa, sp. n. (fig. 3a).

The eyes are wide apart in the male, the frons being about the width of the ocellar tubercle and one-eighth the width of an eye. There are many yellow hairs on the head, pleurae and venter, but dorsally all hairs are black. Only two pairs of presutural acrostichals, and three pairs of marginal scutellar bristles. In addition to the forceps and the accessory plates, the genital cavity is closed by a pair of secondary plates, one lying on each side of those appendages, and the fifth sternite is produced into a pair of downwardly turned chitinous processes. These form a complex that is large and bulbous at the apex of the abdomen, and quite distinctive in appearance. The aedeagus is very short and its strut is broad and stunted. The claspers are not unlike those of *C. bezzii*. The legs are yellow-brown with the coxae more or less, and the anterior femora sometimes slightly, stained with black; the tarsi black.

QUEENSLAND: Brisbane, July and September 1930, 4 males; the female is unknown.

Calliphora sternalis, Mall. (fig. 3b).

C. sternalis, Malloch, Proc. Linn. Soc. N.S.W., lv, 1932, p. 65.

This species is very like *C. deflexa*, from which it differs in having the eyes less wide apart, the frons being one-seventh the width of an eye; nevertheless the ocellar tubercle is proportionally smaller, so that the width of the frons is as wide as the ocellar tubercle. Also the legs have black coxae and femora, and the tibiae are brown; the extreme apex of the femora is usually brown. The chaetotaxy and the colour of the hairs agree with those of *C. deflexa*, as also do the genitalia in the main, but the aedeagus is distinctly longer and varies in small details.

VICTORIA: Seaford and Hastings, i, 1931, 6 males; the female is unknown.

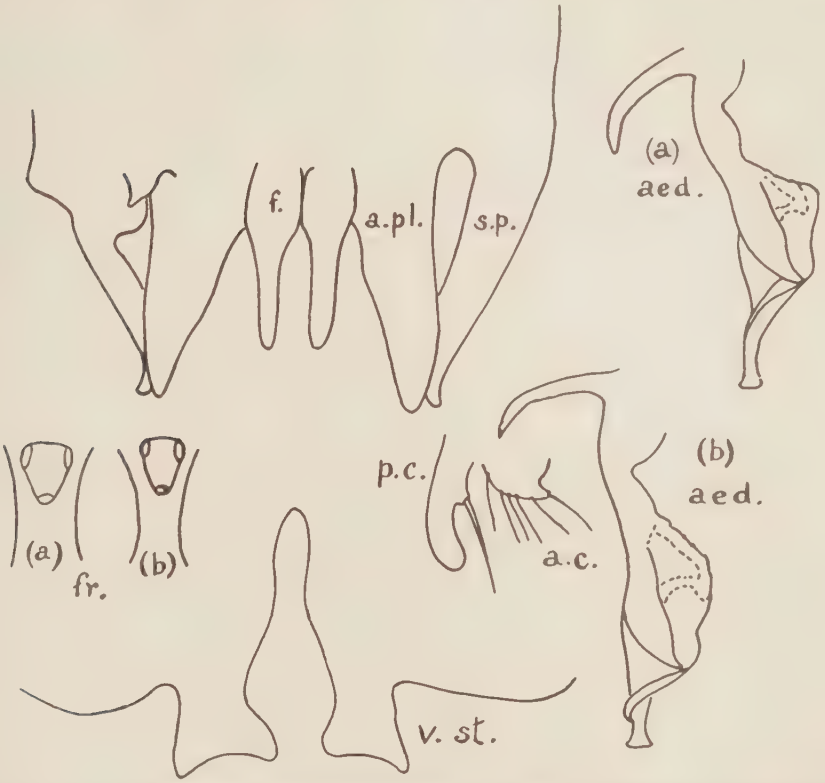


Fig. 3. Male genitalia of *Calliphora deflexa*, sp. n. (a) and of *Calliphora sternalis*, Mall. (b): *aed*, aedeagus; *f*, forceps; *a.pl*, accessory plate; *p.c*, posterior clasper; *a.c*, anterior clasper; *v.st*, fifth sternite; *s.p*, secondary plates; *fr*, frons.

Under this species Malloch refers to a unique male mentioned in my earlier paper which was collected by Dr. I. M. Mackerras. This specimen differs from any other *Calliphora* I have seen in that it has an enormously distended orifice at the apex of the aedeagus, the flange supporting this area being chitinous, not membranous. The species has no relationship with the *sternalis* group.

Malloch has made several errors in interpreting my previous paper, and the chief of these concerns *Pollenia rufipes*, Macq. 1835, which has nothing to do with *Calliphora rufipes*, Macq. 1843; the latter was recorded from Java and is not a member of the genus *Calliphora*.

Subgenus **Proekon.**

Being unable to place the described species of *Proekon* with any assurance, I am forced to restrict descriptions to only four of the species before me, and in doing so I have ventured to suggest the identity of one that was described by Malloch under the name *C. centralis*. That author ignores the only characters that can at present be used for determination, and relies on several inconstant features in the chaetotaxy and colour markings. When his types are returned to Australia in fulfilment of his promise, it will be possible to place the three forms he described in their correct position, bringing them into line with those here dealt with. In the meanwhile I refrain from discussing other forms known to me in case some of them may prove to be the same as Malloch's species.

Some of the species in the subgenera *Neopollenia* and *Proekon* cannot be distinguished on genital characters, though their specific status is readily assured by biological means. One such case is dealt with here, a new name being given for the species that is commonly confused with *C. augur*.

The subgenus *Proekon*, Surc., may be recognised by the abdomen being yellow with a more or less irregular blue-green, blue or blue-black stripe on the dorsal area. The *augur* group contains two known species, and the *centralis* group is a complex which will need further division. So far as yet known, only the former group is associated with the myiasis of sheep, both species under it being implicated.

Key to Species of the Subgenus Proekon.

1. Two presutural acrostichal bristles; segments of abdomen are not margined with blue, except where the dorsal stripe occurs; humeral callus yellow, unlike the dorsum; frons of female much wider than long (*augur* group) 2

   Three presutural acrostichal bristles; first three segments of abdomen margined with a very thin line of metallic colour that extends almost if not quite the whole way across the tergites; frons of female about as wide as long (*centralis* group) 3

2. Eye-frons-eye formula of male 18 : 2 : 18; length of frons to breadth in female as 4 : 5; blue-green abdominal stripe with yellow pulverulence on fourth tergite ... ... *augur*, F.

   Eye-frons-eye formula of male 18 : 3 : 18; frons length to breadth in female as 3 : 5; abdominal stripe vivid blue with white pulverulence on fourth tergite ... ... *nociva*, sp. n.

3. Eye-frons-eye formula of male 16 : 2 : 16; abdominal stripe blue-green and fourth tergite pulverulent; humeral callus yellow, unlike the dorsum ... ... *centralis*, Mall.

   Eye-frons-eye formula of male 28 : 1 : 28; abdominal stripe vivid blue, or toning to blue-black, and entirely without green reflections; fourth tergite without pulverulence; humeral callus concolorous with the dorsum ... ... *falciformis*, sp. n.

All these species have yellow legs, which should be enough to distinguish them from *fuscofemorata*, Mall., whilst I suspect from material before me that *C. macleayi*, Mall., will be found to have the abdomen without the continuous line of metallic colour along the margins of the tergites and the head characters will also differ from those of *C. falciformis*. Some characters used by Malloch to distinguish these species are inconstant and are therefore omitted here.

Calliphora augur, F. (fig. 4).

Musca augur, Fabricius, Syst. Ent., ii, 1775, p. 777.

Calliphora augur (F.) Patton, Phil. J. Sci., xxvii, 1925, p. 400; Hardy, Proc. Roy. Soc. Queensland, xxxvii, 1926, p. 171; Malloch, Proc. Linn. Soc. N.S.W., lii, 1927, p. 310, and liii, 1928, p. 613.

Ochromyia lateralis, Macquart, Dipt. Exot., ii (3), 1843, p. 143.

Proekon lateralis (Macq.) Surcouf, Nouv. Arch. Mus. Paris (5) vi, 1914, p. 112.

Ochromyia nigricornis, Macquart, Dipt. Exot. suppl. 4, 1849, p. 245.

Proekon nigricornis (Macq.) Surcouf, Nouv. Arch. Mus. Paris (5) vi, 1914, p. 114.

Musca dorsalis, Walker, List Dipt. B. Mus., iv, 1849, p. 907.

With regard to the synonymy above, I think there can be little doubt that these names refer to but one species generally accepted under the first name. The descriptions given by Surcouf for *O. lateralis* and *O. nigricornis* agree with *C. augur*, but this remark does not apply to Surcouf's figures, as the proportions of the head differ.

Calliphora oceaniae, Desv., is one of several names that have been placed hitherto under this species, but the species was described from Timor, to which Port Jackson was added. The furthermost north that *C. augur* has yet been traced is central Queensland, and it is not known from any area west of this; moreover in Queensland the fly is a seasonal one, being strictly limited in the Queensland sheep country to the winter, and it does not seem likely that it extends to Timor. All subsequent references given under Desvoidy's name apply to this species and perhaps some of them have included the following one too.

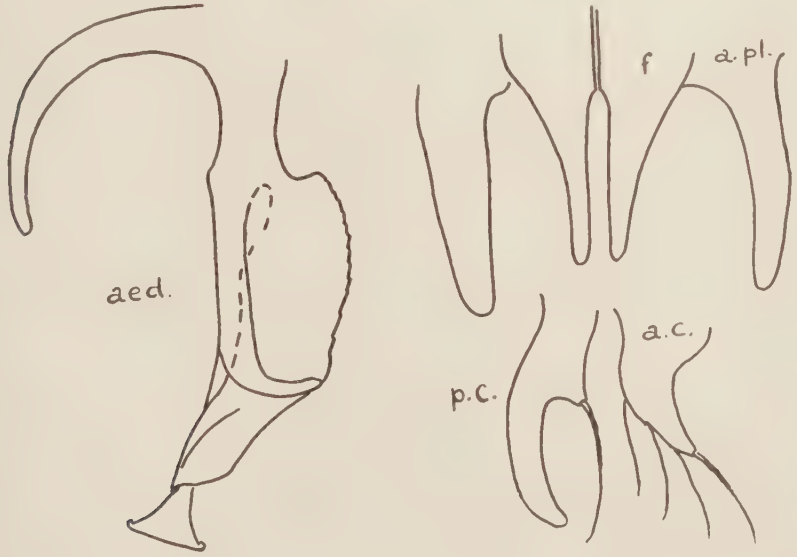


Fig. 4. Male genitalia of *Calliphora augur*, F.: *aed*, aedeagus; *f*, forceps; *a.pl*, accessory plate; *p.c*, posterior clasper; *a.c*, anterior clasper.

The frons in the male is narrow, having the approximate eye-frons-eye formula of 18 : 2 : 18. In the female the length of the frons in proportion to the width is 4 : 5. There are only two presutural acrostichals, and the abdominal stripe is blue-green with the portion on the fourth tergite sometimes quite concealed by a

yellow pulverulent covering. The marking on the fourth tergite varies from semi-circular to trapezoidal, and is always rather large. The black on the thorax does not invade the humeral callus, which is therefore usually yellowish.

The aedeagus (fig. 4) has a well-developed funnel-shaped apex and a strong, simply curved strut ; the claspers are also quite normal, the bristle on the posterior one arising from a prominence. The forceps and accessory plate are also simple and normal. In general features these do not differ much from those of *C. fallax*, Hardy.

Queensland, New South Wales, Victoria, Tasmania.

In Queensland, the species seems to be eliminated in normal years during the early summer months. It may possibly survive in limited numbers under favourable conditions of climate, but experiments show it to be heavily subjected to disease during hot weather. In these experiments it was found that the carrion became putrid so rapidly that its state of decay was too advanced for the maggots. They could not successfully breed in it. When this happens before they have time to complete feeding, they may subsequently leave the carrion fully fed and in apparently healthy condition, but the skin of the maggot turns brown in patches instead of forming the puparium, and the maggot dries out in a leathery flat strip of thickened cuticle. All Calliphoras seem to be subject to death in this manner during summer, some being more prone to the disease than others ; and further experiments conducted during winter under incubation induced the same type of disease in the genus *Lucilia*. This may account for the disappearance in Queensland of flies that normally breed in the southern States.

Calliphora nociva, sp. n.

This species is so closely allied to *C. augur* that it has been allowed to stand under the same name. So far as I am aware, O. W. Tiegs was the first to perceive the difference somewhere about 1921, and I have a specimen before me that indicates this on the label. Tiegs considered it to be probably identical with *C. augur*, but further material was desirable before he could be sure. In the summer of 1930–1931. I took the opportunity when visiting the southern States to ascertain the status of this form, and have concluded that it is a distinct species.

The frons of the male has the approximate eye-frons-eye formula of 18 : 3 : 18, In the female the length of the frons in proportion to the breadth is 3 : 5. The humeral callus is yellowish and there are only two presutural acrostichal bristles. The abdominal stripe is vivid blue, and the portion on the fourth tergite is never concealed although covered with a silvery or ashy white pulverulent overlay. The marking on the fourth tergite is rather trapezoidal and may cover or appear to cover the whole tergite. The aedeagus, forceps, accessory plate and claspers, are as in *C. augur*.

South Australia : Adelaide, 6 males, 19 females ; Eden Valley (sheep country), 1 female ; Meningie, 13 males, 32 females. Victoria : Culgoa, 3 males, 2 females ; Ouyen, 1 female ; Melbourne, 1 female. New South Wales : adjacent to the Federal Capital Territory, where it is well recognised as a seasonal species. All specimens in the type series were taken during January 1931.

It is evident that this fly is a seasonal one in most parts of Victoria, New South Wales and at Canberra, but along the coastal area of South Australia it would seem to be permanently established and becomes a pest inland, attacking sheep, though usually rare in the sheep country during the warmer months of the year. This fly occurs in the open bush and in certain types of Mallee. As it was entirely absent in the patches of Mallee visited by me around Adelaide, I suspect certain necessary features were missing there, but I found it plentiful enough on tree-covered ground in the plains beyond Claredon ; here males occurred, these being the only ones of their sex that I could find in the Adelaide district.

Calliphora centralis, Mall. (fig. 5).

C. centralis, Malloch, Proc. Linn. Soc. N.S.W., lii, 1927, p. 311.

The characters given by Malloch for the recognition of this species are not very helpful, but I believe his type will be found to conform to the species here described. Curran, in 1929, recorded a specimen from New Caledonia under this name ; if it be rightly determined, the discovery may prove important.

The frons of the male has the eye-frons-eye formula of 16 : 2 : 16, that of the female being about as wide as long. There are three presutural acrostichals and the abdominal stripe is blue-green. The humeral callus is yellow. The fourth tergite may be largely covered with the green colour, or it may be reduced to a large or small triangular area, or even to a very narrow strip, and sometimes it is not at all apparent. A white or a yellow pulverulent overlay is nearly always very perceptible on the fourth tergite, and the three anterior tergites are margined with a line of metallic blue-green.

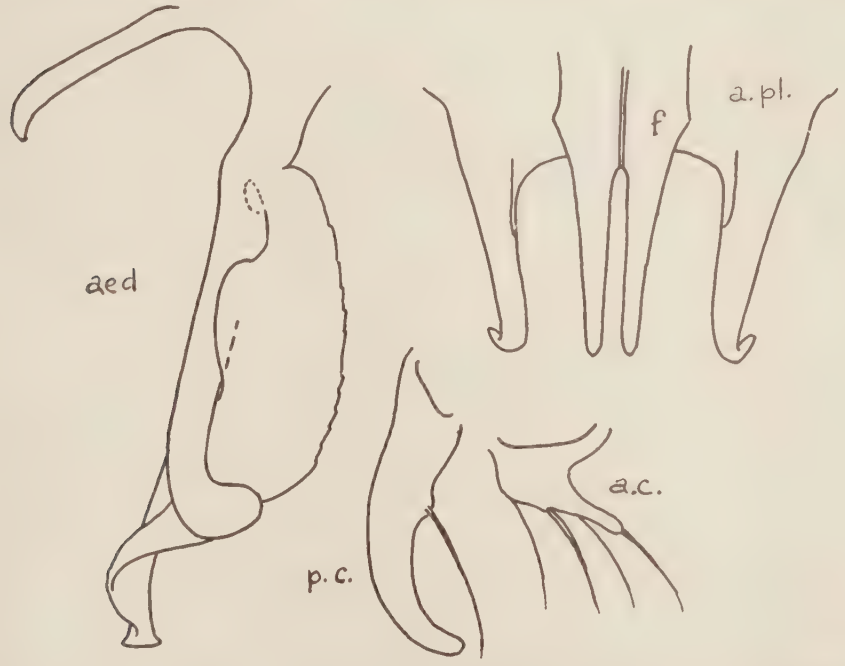


Fig. 5. Male genitalia of *Calliphora centralis*, Mall. : *aed*, aedeagus ; *f*, forceps ; *a.pl*, accessory plate ; *p.c*, posterior clasper ; *a.c*, anterior clasper.

The aedeagus (fig. 5) has its strut very straight till near the apex, where it takes a sharp but short bend, the apex being broadly rounded. The accessory plates are strongly curved at their apex, but in other respects the genitalia are normal.

QUEENSLAND : Brisbane, throughout the year.

This is an open forest species that has been known to me since 1926, but for some time I had only the female. Males rest on twigs at about sunset and are easily discovered in this way, whereas the females seem almost invariably to be confined to the ground, occasionally visiting flowering shrubs, and are best sought for by discovering the whereabouts of the male first, then searching on the ground around the area. It does not seem to be attracted to baits normally like other species, even where it occurs plentifully. My series consists of over sixty specimens.

Calliphora falciformis, sp. n. (fig. 6).

This a very distinct species, although in some of its characters it seems to agree with *C. macleayi*, Mall. From that species it is likely to be distinguished by its quite normal light colour, for Malloch describes the head of *macleayi* as being dark, as in his *C. fuscofemorata*.

In the male the eye-frons-eye formula is 28 : 1 : 28, the eyes being very close together. The frons of the female is about as wide as long. There are three presutural acrostichals and the abdominal stripe varies from blue-black to very vivid blue, the latter being the normal colour. The fourth tergite may be almost completely covered with blue, especially in the female, but may range down to a large triangular area that usually reaches the hind-margin. It is entirely without a pulverulent overlay, but the apical border of three segments has a linear metallic margin. The humeral callus is concolorous with the dorsum of the thorax.

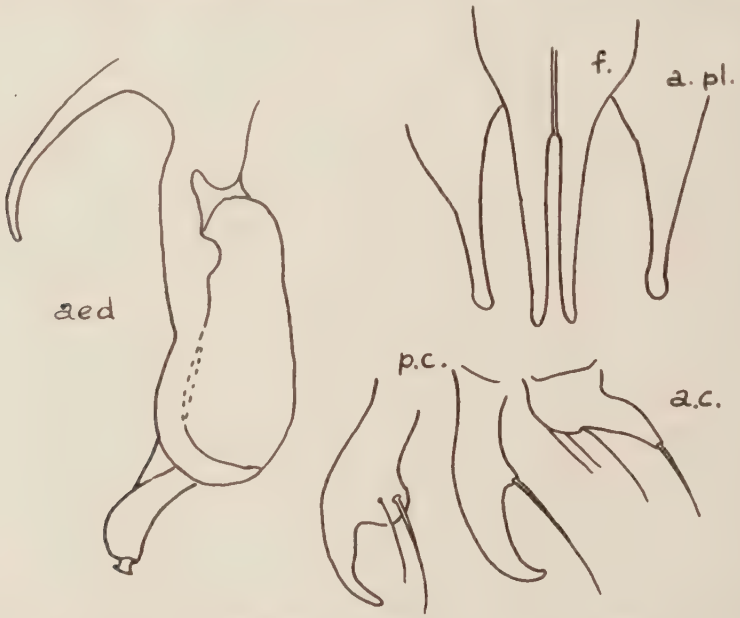


Fig. 6. Male genitalia of *Calliphora falciformis*, sp. n.; *aed*, aedeagus; *f*, forceps; *a.pl*, accessory plate; *p.c*, posterior clasper; *a.c*, anterior clasper.

The aedeagus (fig. 6) has its strut somewhat sickle-shaped, the specific name being based on this apparently unique character. The funnel-shaped apex is very small, smaller than in any other species I have examined. Other characters are more or less normal, and the accessory plate is slightly widened and rounded at the apex.

Queensland: Mt. Glorious, 5 males and 8 females, iv, 1930 and i, 1932; Brisbane Botanical Gardens, 1 female.

This is a rain-forest frequenting species which I found to be rather plentiful in January at Mt. Glorious. It came quite readily to lure, being the only species of *Proekon* to do so. Apparently it was not present in any great numbers, for apart from luring it was not seen. A single pair taken in April was caught on the wing. The specimen from the Botanical Gardens was evidently a stray, for no more have been discovered there.

MOSQUITO NOTES.—XI.

By F. W. Edwards.

Contents.

I. A remarkable *Uranotaenia* larva from Hong Kong.

II. A new *Theobaldia* from the Azores.

III. New African Culicines.

I. A remarkable *Uranotaenia* Larva from Hong Kong.

In the autumn of 1931 I received for determination from Dr. R. B. Jackson a small number of Culicine larvae collected in Hong Kong. These included two specimens of a *Uranotaenia* with very remarkable antennae, which seem well worth describing as a further example of the striking and unexpected deviations of structure which occur in various members of this genus. As the specimens sent were whole larvae and not skins, the identity of the species is somewhat uncertain, but an adult of *U. testacea*, Theo., was obtained by Dr. Jackson at the same time as the larvae, and it is most probable that the larvae belong to that species. Incidentally, *U. testacea* has not been recorded from Hong Kong before.



Fig. 1. *Uranotaenia testacea*, Theo. (?), head of larva, from Hong Kong: *a*, frontal spine, further enlarged; *b*, antenna from beneath, further enlarged; *c*, pecten teeth.

The antennae of the species of *Uranotaenia* hitherto known are more or less similar in type, having a fine single or slightly branched hair on the shaft, and four apical bristles of varying length in addition to the usual papilla; the shaft may or may not bear spicules, and the shaft hair may be well before, at, or somewhat beyond

the middle. In the new larva the short antenna bears three conspicuous flattened plates, one near the middle and two at the tip. At first sight these plates seem to represent the shaft-hair and two of the apical (or subapical) bristles, but a closer inspection shows that the plate at the middle of the antenna is situated on the lower surface, a position in which the shaft-hair is never found, this hair being either dorsal or external. Moreover, in the Hong Kong larva there is a membranous area on the lower surface extending from the insertion of the median plate to the tip of the antenna, and on the dorsal surface there is a small simple subapical hair. The plate at the middle of the antenna must therefore be derived from one of the apical bristles, and the antenna is peculiar not only in the form of the "apical" bristles, but in the retraction of one of them to the middle and the shifting of the shaft-hair to a subapical position.

Apart from the form of the antennae, the Hong Kong larva shows all the main features of a typical *Uranotaenia*, notably the flattened form of the four frontal hairs, the excavation of the front margin of the clypeus between the two clypeal spines, and the presence of lateral chitinous plates on the eighth segment. The main features, apart from the antennae, which are probably of importance for specific diagnosis are as follows :—

Clypeal spines long and not very stout. Frontal spines blackened, much flattened and finely fringed. Innermost pronotal hairs set in small but distinct plates which lie rather close together (this is the condition found in most typical *Uranotaenia*, but in some species the plates are indefinite and wide apart). Hairs of propleural group inconspicuous, one longer than the others but shorter than usual. Meso- and meta-thoracic plates rather small. Abdomen practically bare dorsally, with long lateral hairs only on the first three segments. Plates of eighth segment connected by a dorsal saddle ; comb-teeth sharp-pointed, smooth, about four in number. Siphonal index about 2·5, large tuft near middle, 8–10 branched, valves large. Pecten teeth about 10 in number, of rather unusual form, being widened and fringed on the apical margin only. Anal segment ringed, posterior margin of plate spinulose, lateral hair small and simple, about six bifid or trifid hairs in the ventral brush.

II. A new *Theobaldia* from the Azores.

The mosquito fauna of the Atlantic Islands is scanty but interesting. Our knowledge of the species occurring in Madeira and the Canary Islands has recently been summarised by Christophers, from whose work we learn that 12 species occur in the Canaries and 5 in Madeira. Several of these species show more or less well-marked varietal differences from forms occurring in Spain or North Africa, but only one species is endemic, this being *Aëdes eatoni*, Edw., of Madeira, which is quite distinct from any species known in Europe. It now appears that a second endemic Atlantic Culicine exists in the Azores.

So far as I am aware *Culex pipiens* is the only mosquito hitherto recorded from the Azores, this having been described by Theobald (under the names *C. azoriensis* and *C. varioannulatus*) from specimens collected by Dr. M. Grabham. In 1929 Mr. J. Balfour-Browne made a collecting trip to the island of Pico, and in addition to *C. pipiens* obtained examples of the new *Theobaldia* described below.

Theobaldia atlantica, sp. n.

♀. *Head* with the erect scales black, decumbent scales mostly yellowish. Proboscis and palpi black, with few or no scattered pale scales, palpi narrowly whitish at tip. *Thorax* black ; mesonotal scales mostly black, with a few golden scales intermixed, latter tending to form a pair of small spots in middle. *Abdomen* mainly black ; tergites with small basal lateral white spots which are scarcely visible dorsally ; second tergite without median white line ; venter also largely blackish.

Legs black, without scattered pale scales. Femora with preapical yellowish ring, faint on front and middle legs but distinct on hind legs. Tibiae without pale scales even at tip. Front and middle tarsi with very narrow yellowish rings at bases of first two segments, hind tarsi with broader (but still narrow) yellowish rings at bases of first three segments, also (in some specimens) at base of fourth. *Wings* somewhat smoky, scales all black; the usual aggregations of scales on cross-veins and at bases of forks. A darker patch on membrane below base of *Rs* (as in other species) but none between bases of forks (such as occurs in *T. maccrackenae*). Halteres with black knob. Wing-length 5–7 mm.

AZORES: Ilha da Pico, Serra Gorda, vii. 1929, 5♀ (*J. Balfour-Browne*).

T. atlantica differs from any European species of the genus not only in its general black colour, but also in possessing pale subapical rings on the femora while lacking a median pale ring on the first segment of the hind tarsus. The Mexican *T. maccrackenae*, D. & K., also combines these last two features, but differs in several other respects. The pale rings of the hind tarsi are narrower than in any other species of the group.

III. New African Culicines.

The following are brief diagnoses of new species of African Culicines recently received at the British Museum. A fuller account of them will be given in the forthcoming monograph of the mosquitos of the Ethiopian Region, now in preparation by Dr. A. M. Evans, Mr. G. H. E. Hopkins and the present writer.

Uranotaenia shillitonis, sp.n.

A rather large dark species, almost uniformly dark brown, without special ornament on body or legs, and without any unusual features in the legs of the male; head dark, with whitish orbits; pronotal lobes with white scales; pleurae largely pale brown with some dark markings; venter pale. Wing-scales all dark, moderately broad; fork-cells longer than usual, upper fork over half as long as its stem. Differs from all other species of the genus in having *all* the mesonotal scales broad and flat, but there are no white scales in front of the wing-base. Wing-length 3 mm.

UGANDA: Nyakasura (*J. F. Shillito*). Larva in reeds and bamboos.

Uranotaenia hopkinsi, sp. n.

A small dark species which by Philip's key to the Ethiopian species of this genus would run to *U. candidipes*, Edw.; as in that species, the hind tarsi have the last 2·5–3 segments pure white, but the new species differs from *U. candidipes* as follows: Head with a narrow orbital line of blue scales. Upper half of pleurae somewhat darkened, but not strikingly contrasted with the pale lower half. Abdominal tergites entirely dark brown. Femora and tibiae without white spots at tip. Front and middle tarsi only indistinctly pale on the last three or four segments. Wing-scales narrower. Wing-length 2 mm.

UGANDA: Kampala (*G. H. E. Hopkins*).

Ficalbia (Mimomyia) perplexens, sp. n.

Closely resembles *F.* (*M.*) *hispida*, Theo., from which it differs (as adult) chiefly in the colour of the flat scales of the head, which are blackish instead of pale yellow. Mesonotum black, strongly contrasting with the pale yellow pleurae, the latter without any trace of darkening above. First abdominal tergite with only a small patch of black scales in middle; remaining tergites with small lateral basal yellowish areas. Hind femora very extensively yellow on anterior surface, with only a narrow dark dorsal line, except on distal fourth, which is more extensively dark. Only female and larva yet obtained, the latter differing greatly from those of *F. hispida*.

UGANDA: Kampala (*G. H. E. Hopkins*).

Culex hopkinsi, sp. n.

Belongs to the *pipiens* series; most closely allied to *C. andersoni*, Edw., which it resembles in having all the femora almost entirely black-scaled, differing in the longer and more hairy male palpi (these exceeding the proboscis by fully the length of the last segment), and more especially in having the scales of the head and mesonotum uniformly pale golden. Hypopygium almost as in *C. andersoni*, with a slight difference in the teeth of the phallosome. Wing-length 4·5–6 mm.

Uganda: Kameranjoka, Ruwenzori foothills (*G. H. E. Hopkins*).

Culex musarum, sp. n.

Belongs to the *pipiens* series; intermediate between *C. andersoni*, Edw., and *C. hancocki*, Edw., resembling the latter in thoracic ornamentation and the former in the more extensively black femora. Palpi of ♂ only slightly hairy and not much longer than proboscis. Mesonotum of ♀ with a distinct ornamentation of pale scales, comprising a median stripe and a rather broad border on anterior half, and a pair of stripes on posterior half; these markings much less obvious in ♂, and less sharply defined than the similar markings of *C. hancocki*. Abdominal tergites of ♀ with the pale basal bands very narrow or reduced to lateral spots; sternites with broad black apical bands. Front and middle femora almost all black; hind femora with the white scales confined to under-surface on basal half or less. Hypopygium of ♂ much as in *C. andersoni*, phallosome differing slightly. Wing-length 3–4 mm.

Uganda: Fort Portal (*H. Hargreaves*; *J. F. Shillito*); Kampala and Lira (*G. H. E. Hopkins*). Larvae in leaf-axils of wild banana.

As in *C. hancocki* the median pale stripe of the mesonotum is confined to the area between the two bare lines. In the rather similar *C. scotti*, Theo. (Seychelles Is.) pale scales occur also outside the bare lines.

Aëdes (Aëdimorphus) leesoni, sp. n.

Closely allied to *A.* (*A.*) *alboventralis*, Theo., differing mainly if not solely in the male hypopygium. Style broad apically, with a terminal row of flattened spines and a pubescent process much as in *A. alboventralis*, *A. abnormalis* and *A. rhecter*, from all of which it differs in the presence of a long, curved, sharp-pointed process from the middle of the dorsal margin.

S. Rhodesia: Shamwa (*H. S. Leeson*; type). Bechuanaland: Gaberones (*D. Drew*).

Aëdes (Aëdimorphus) natronius, sp. n.

Closely resembles *A.* (*A.*) *durbanensis*, Theo., the only apparently constant external difference being that the pale basal bands of abdominal tergites 3 and 4 are yellow in the middle instead of white right across. Hypopygium of ♂ differing from *A. durbanensis* and all other members of the subgenus in having the style simple, with long terminal spine, as in *Stegomyia*; coxite also resembling *Stegomyia* in the presence of a large basal plaque fringed with long hairs.

Uganda: Mwaya and Kitoma, Lake Bogosu and Lake Maseche (*L. Beadle*). Kiborna and Lake Bogosu (*Dr. R. E. McConnell*; previously recorded as *A. durbanensis*). Larvae in alkaline pools.

THE DETERMINATION OF THE AGE OF *ANOPHELES* BY DIFFERENCES IN THE SIZE OF THE COMMON OVIDUCT.

By G. Mer,

Malaria Research Station (Rosh Pinah), Department of Hygiene, Hebrew University, Jerusalem.

The length of life of the adult female *Anopheles* is an important factor in the epidemiology of malaria. Theoretically malaria transmission is possible only if the Anophelines live longer than it takes the parasite to complete its sexual cycle. It is even conceivable that a dense *Anopheles* population and many human carriers may fail to cause an epidemic if the life of the vector were less than 10–12 days. The longer the *Anopheles* female lives, the greater chance it has to become infected and infective and the more persons it will be likely to infect.

Notwithstanding the importance of determining the length of life of the Anophelines at various seasons of the year and its relation to the epidemiology of malaria, few attempts have been made in this direction. Most authors have tried to determine the length of life of *Anopheles* by their viability under laboratory conditions. Such data, however, have only a limited significance, and it seemed desirable to find some method of age determination in Anophelines caught in nature.

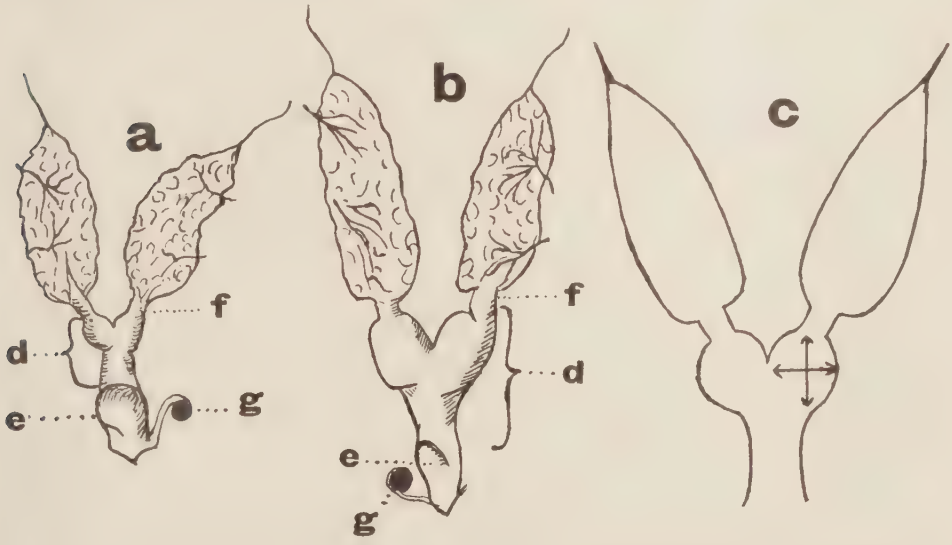


Fig. 1. *A. elutus*, Edw., oviduct; *a*, before pairing; *b*, after oviposition; *c*, method of measuring ampulla; *d*, common ovarian duct; *e*, bursa copulatrix; *f*, paired ovarian duct; *g*, spermatheca.

Christophers in 1911 found that in some Anopheline females it is possible to differentiate the multiparous from the nulliparous. He found that (*a*) in some of the Anopheline females that have laid eggs a few ripe ova remain in the ovary, and (*b*) the ovaries of females that have laid at least once are different from those of the virgin female, because the second set of follicles develops slowly during the ripening of the ova belonging to the first set.

Repeating the observations of Christophers we have found that only in a small percentage of females ripe ova are left after egg-laying (in our examination in 27 out of 264 or 10%), and that it is impossible to ascertain why this phenomenon takes place in some and not in others. The differences in the ovaries which were observed by Christophers can be seen only in Anophelines containing neither blood nor ova. The number of such females varies and the ratio of old to new females depends not only on the respective numbers, but also on other factors, such as the time of the night when they come from the breeding-places and the possibility of getting food during the night of arrival. It is clear, therefore, that a method for differentiating between old and new females that would be applicable to a large percentage of the females caught would be exceedingly useful.

In the course of the dissections it was found that in *A. elutus* females the common oviduct undergoes considerable changes during gravidity, and that these changes are not reversible and may consequently serve to differentiate old females from new ones.

The proximal portion of the common oviduct of *A. elutus* presents two dilatations, divided from each other by an upper median depression. The oviducts open into these dilatations or ampullae. In virgin females (fig. 1, *a*) the ampullae are small and well delimited from the rest of the common oviduct (distal portion), but only slightly so from one another. During the first gravidity the ampullae increase in size, being largest during egg-laying and at the same time become more clearly divided from each other; this distribution is at the expense of the paired oviducts, which become shorter. The important point is that these changes persist after egg-laying (fig. 1, *b*), being unaffected by subsequent gravidities, notwithstanding the fact that the ovary practically regains its former volume.

TABLE I.

Size of Common Oviduct in overwintering fat Females of Anopheles elutus *kept in the Laboratory.*

Surface of the ampulla in 1/16 mm.²		1–5	5–10	10–15	15–20	20–25	25–30	30–35	35–40	More than 40
Groups	No. dissected									
I No signs of egg-development ...	54	25	29							
II Ovaries, stage 2 ...	41	6	31	4						
III Ovaries, stage 3 ...	11	—	1	9	1					
IV Ovaries, stage 4 ...	29	—	—	6	21	2				
V Ovaries, stage 5 ...	11	—	—	1	4	6				
VI After 1st egg laying (24 or 48 hours)	45	—	—	—	1	25	19			
VII After 2nd egglaying (24 or 48 hours)	15	—	—	—	—	4	7	2	—	2

This phenomenon was tested in the laboratory in a number of *A. elutus* females. Virgin females were fed on blood and then dissected at various stages of egg-development, after egg-laying and during the second gravidity. For comparison a number of them were dissected before the blood feed. Since it was impossible to bring about copulation in captivity, overwintering females with fat reserves were used for these experiments.

In addition a number of *A. clutus* females caught in nature during the breeding season were dissected before and after egg-laying in the laboratory and their common oviducts compared. For all of these measurements mosquitos of approximately the same size were used, measurements of exceptionally large or small specimens being discarded.

The results of these measurements are summed up in Tables I and II. Two diameters of one of the ampullae (the largest one if they were not equal) were measured as shown in fig 1, *c* and the surface area calculated. The dissection was carried out in distilled water in the following way: The mosquito was placed on a slide on its back; one of the pleurae was stripped down from the 5th to the 8th abdominal segment; the midgut was then separated from the hind gut, the tracheal connections of the ovary cut and the hind gut torn away together with the 9th segment. The common oviduct could then be gently separated from the ventral plate of the 7th abdominal segment. These precautions are necessary to prevent distortion of the duct. The stages of egg-development were noted according to Christophers. The measurements were carried out with an ocular micrometer under a Leitz binocular, 0c.10, obj. 2.

TABLE II.

Differentiation of old and new Females of A. elutus (*captured specimens*) *by Size of the Common Oviduct.*

Surface of the ampulla in 1/16 mm.²			1–5	5–10	10–15	15–20	20–25	25–30	30–35	35–40	More than 40
State of ovaries	No. dissected	Diagnosed age of females									
No signs of egg-development	8	New ...	3	4							
		Doubtful									
		Old ...								1	
Ovaries stage 2	39	New ...		4	11						
		Doubtful									
		Old ...					4	6	4	6	4
Ovaries stage 3	29	New ...			4	2					
		Doubtful					2				
		Old ...					2	8	5	2	4
The same group after egglaying	31						3	7	7	5	9
Meagre with few eggs left over	23						4	11	6	2	

These measurements show that in *A. elutus* females with ovaries not beyond stage II and III, that is in the early stages of egg-development, it is possible to distinguish the nulliparous from the multiparous by measuring the area of the common oviduct. In new mosquitos the ampullae are rarely above $15\frac{1}{16}$ mm.², while in old mosquitos they are always above 20. In most cases exact measurement is not necessary, the difference being quite obvious to a trained eye.

Summary.

A procedure is described which makes it possible to differentiate nulliparous from multiparous *A. elutus* and hence newly hatched from old mosquitos.

Reference.

CHRISTOPHER, 1928. "How to do a Malaria Survey." Health Bulletin No. 14, Malaria Bureau, No. 8.

COLLECTIONS RECEIVED.

The following collections were received by the Imperial Institute of Entomology between 1st July and 30th September, 1932, and the thanks of the Managing Committee are tendered to the contributors for their kind assistance :—

Mr. M. D. Austin :—23 Parasitic Hymenoptera ; from England.

Mr. E. Ballard, Government Entomologist :—2 species of Coccidae and 20 Ticks ; from Palestine.

Dr. H. F. Barnes, Rothamsted Experimental Station :—5,200 Parasitic Hymenoptera ; from England.

Mr. A. H. Bastin :—2 Geotrupidae ; from Belgium.

Dr. M. Bensaude :—24 Lepidopterous pupae ; from Portugal.

Mr. H. J. Brédo :—10 Diptera, 109 Parasitic Hymenoptera and 50 pupa-cases, 79 Lepidoptera and 6 pupa-cases, 2 species of Coccidae, and 78 Orthoptera ; from the Belgian Congo.

Mr. L. L. Buchanan :—20 Coleoptera ; from Cuba.

Mr. G. Bünzli :—300 Formicidae and 15 species of Coccidae ; from Surinam.

Dr. M. Burr :—2 Hymenoptera, 4 Rhynchota, and 54 Orthoptera ; from Spain.

Chief Entomologist, Pretoria :—96 Parasitic Hymenoptera and 2 speciesof Aleurodidae ; from South Africa.

Mr. A. F. Clark, Cawthron Institute :—5 Coleoptera ; from New Zealand.

Mr. G. H. Corbett, Government Entomologist :—42 Diptera, 44 Coleoptera, 55 Parasitic Hymenoptera, 18 other Hymenoptera, 66 Lepidoptera, 260 Isoptera, 6 species of Coccidae, 21 other Rhynchota, and 3 Psocidae ; from Malaya.

Dr. J. F. Corson :—3 hybrid *Glossina* and 3 puparia ; from Tanganyika Territory.

Coryndon Memorial Museum, Nairobi :—237 Coleoptera ; from Kenya Colony.

Mr. G. S. Cotterell, Government Entomologist :—7 Diptera, 4 Parasitic Hymenoptera, and 39 Lepidoptera ; from the Gold Coast.

Mr. A. Cuthbertson, Assistant Entomologist :—6 *Stomoxys*, 117 other Diptera, 7 Coleoptera, 6 Hymenoptera, 74 Rhynchota, and 6 Orthoptera ; from Southern Rhodesia.

Dr. E. Dallas :—13 Lepidoptera ; from the Argentine.

Director, Deli-Proefstation :—7 Coleoptera, 3 Lepidoptera, and 6 Rhynchota ; from Sumatra.

Director of Veterinary Services, Kampala :—26 Tabanidae and 11 *Stomoxys* ; from Uganda.

Mr. L. H. Dunn :—30 Simuliidae ; from the Panama Canal Zone.

Mr. P. R. Dupont, Director of Agriculture :—3 Lepidoptera and 3 larvae ; from the Seychelles.

Mr. W. H. Edwards, Government Entomologist :—6 Coleoptera and 12 Rhynchota ; from Jamaica.

Dr. H. Eltringham :—60 Lepidopterous early stages ; from England.

Dr. H. J. de Fluiter :—50 Parasitic Hymenoptera ; from Holland.

Mr. J. L. Froggatt, Government Entomologist :—21 Diptera, 80 Coleoptera, 12 Parasitic Hymenoptera, 8 other Hymenoptera, 19 Lepidoptera, 32 Rhynchota, and 16 Orthoptera ; from New Guinea.

Dr. A. B. Gahan :—7 Parasitic Hymenoptera ; from New South Wales.

Mr. J. C. M. Gardner, Systematic Entomologist :—131 Parasitic Hymenoptera, 25 other Hymenoptera, and 24 Psyllidae ; from the United Provinces, India.

Mr. S. Garthside :—3 Diptera, 12 Parasitic Hymenoptera and 9 cocoons ; from England.

Capt. F. F. Gass :—172 Lepidoptera ; from India.

Mr. J. Ghesquière :—120 Coleoptera ; from the Belgian Congo.

Mr. E. G. Gibbins :—4 *Phlebotomus* and 90 Chironomidae ; from Uganda.

Government Entomologist, Lyallpur :—11 Rhynchota ; from the Punjab.

Miss L. F. Graham :—16 Parasitic Hymenoptera ; from Australia.

Prof. G. Grandi :—5 Parasitic Hymenoptera ; from Italy.

Mr. M. Guilis :—75 Parasitic Hymenoptera ; from Spain.

Mr. G. J. Haeussler :—16 Parasitic Hymenoptera and 14 cocoons ; from France.

Mr. G. L. R. Hancock, Assistant Entomologist :—179 Diptera, 135 Coleoptera, 11 Parasitic Hymenoptera, 11 other Hymenoptera, 220 Lepidoptera, 4,500 Thysanoptera, 212 Rhynchota, and 5 Orthoptera; from Uganda.

Mr. G. H. Hardy :—9 Diptera ; from Australia.

Mr. E. Hargreaves, Government Entomologist :—2 Culicidae, 32 other Diptera, 52 Coleoptera, 200 Parasitic Hymenoptera, 206 other Hymenoptera, 72 Lepidoptera, 50 Isoptera, 4 species of Coccidae, 1 species of Aphidae, 11 other Rhynchota, 30 Orthoptera, 3 Dermaptera, 40 Trichoptera, and 150 Mites ; from Sierra Leone.

Mr. W. D. Hincks :—87 Coleoptera ; from various localities.

Imperial Chemical Industries, London :—2 species of Coccidae; from Japan.

Imperial Institute, London :—30 Cynipid early stages ; from Palestine.

Dr. H. C. James, Assistant Entomologist :—24 Parasitic Hymenoptera ; from Kenya Colony.

Mr. H. B. Johnston :—8 Diptera, 459 Coleoptera, 2 Parasitic Hymenoptera, 239 other Hymenoptera, 6 Lepidoptera, and 76 Orthoptera ; from the Sudan.

Mr. C. B. R. King, Tea Research Inst. :—35 Parasitic Hymenoptera and 17 cocoons ; from Ceylon.

Mr. L. A. L. King :—14 Diptera ; from Scotland.

Mr. K. B. Lal :—3 Chalcididae ; from Scotland.

Dr. W. A. Lamborn, Medical Entomologist :—270 Diptera, 49 Coleoptera, 66 Parasitic Hymenoptera and 15 cocoons, and 11 Lepidoptera ; from Nyasaland.

Mr. L. Laspes :—6 Coleoptera ; from Morocco.

Mr. O. B. Lean :—3 *Tabanus*, 4 *Glossina*, 46 Coleoptera, 6 Hymenoptera, 4 Lepidoptera, 26 Rhynchota, and 2,215 Orthoptera ; from the French Sudan.

Prof. A. G. Lebedev :—220 Lepidoptera ; from Russia.

Dr. S. Leefmans :—70 Coleoptera, 81 Lepidoptera, 3 Rhynchota, and 6 Orthoptera ; from the Dutch East Indies.

Mr. R. A. Lever, Government Entomologist :—4 Nycteribiidae, 5 Culicidae, 4 Tabanidae, 43 other Diptera, 205 Coleoptera, 31 Parasitic Hymenoptera, 112 other Hymenoptera, 24 Lepidoptera, 50 Isoptera, 33 Rhynchota, 6 Orthoptera, 8 Odonata, 200 Mites, 4 Scorpions, 2 Snakes, 2 Birds, and 4 Bats ; from the Solomon Islands.

Mr. E. A. Lewis, Veterinary Entomologist: —4 Tabanidae, 2 *Stomoxys*, 36 other Diptera, 35 Dipterous early stages, 32 Coleoptera, 2 Rhynchota, and 16 Orthoptera ; from Kenya Colony.

Dr. A. Da Costa Lima :—16 Coleoptera ; from Brazil.

Dr. Ll. Lloyd :—125 Chironomidae ; from England.

Mr. J. B. Loughnane :—1 species of Aphidae ; from Ireland.

Dr. E. A. Lumbey :—A pair of Locust wings ; from Arabia.

Dr. J. W. Scott Macfie :—300 Diptera ; from Italy and the Balearic Islands.

Dr. G. Martelli :—4 Braconidae ; from Italy.

Prof. F. J. Meggitt :—2 *Chrysops*, 12 other Diptera, 41 Coleoptera, 5 Hymenoptera, 15 Rhynchota, 11 Orthoptera, 2 Dermaptera, and 2 Myrmeleonidae ; from Burma.

Dr. D. Miller, Cawthron Institute :—10 Jassidae and 3 slide preparations ; from New Zealand.

Mr. M. C. Mossop, Assistant Entomologist :—9 Coleoptera, 28 Parasitic Hymenoptera, and 4 Lepidoptera ; from Southern Rhodesia.

Dr. C. F. W. Muesebeck :—7 Parasitic Hymenoptera ; from the United States of America.

Mr. J. Muggeridge, Government Entomologist :—200 Mites and 5,000 Eelworms from New Zealand.

Dr. J. G. Myers :—11 Parasitic Hymenoptera ; from Florida.

Natal Museum, Pietermaritzberg :—1 Anthomyiid ; from South Africa.

Pacific Entomological Survey : 2,446 Coleoptera and 144 early stages, 60 Aleurodidae, 100 Psocidae, 500 Planipennia and 40 early stages ; from the Marquesas and Society Islands.

Mr. H. M. Pendlebury, F.M.S. Museum :—90 Coleoptera and 20 larvae, 850 Parasitic Hymenoptera and 200 cocoons ; from Malaya.

Dr. S. V. P. Pill :—2 Coleoptera, 2 Hymenoptera, 3 Lepidoptera, and 95 Orthoptera ; from South Persia.

Mrs. M. C. Rant :—82 Orthoptera ; from Arabia.

Mr. Y. R. Rao :—45 Orthoptera ; from Baluchistan.

Mr. D. M. Reid :—3 Parasitic Hymenoptera ; from Scotland.

Dr. A. Reyne :—2 Orthoptera ; from the Dutch East Indies.

Dr. W. E. Ripper :—92 Parasitic Hymenoptera ; from Austria.

Mr. T. A. Russell, Plant Pathologist : 4 Parasitic Hymenoptera and 4 cocoons, 9 Lepidoptera and 4 early stages, and 40 Thysanoptera ; from Bermuda.

Dr. H. Sachtleben :—12 Parasitic Hymenoptera ; from Germany.

Nihat Schewket Bey : -10 Diptera, 29 Coleoptera, and 10 Lepidoptera ; from Turkey.

Dr. W. S. Shaw :—12 Coleoptera ; from South India.

Mr. H. W. Simmonds, Government Entomologist : 7 Coleoptera and 24 Parasitic Hymenoptera ; from the Fiji Islands.

Prof. Y. S. Sjöstedt :—87 Parasitic Hymenoptera ; from China.

Dr. C. Strickland :—4 Millipedes ; from Assam.

Dr. J. M. Swaine :—2,000 mites ; from Canada.

Dr. P. Tchorbadjiev :—4 Diptera, 39 Coleoptera, 65 Parasitic Hymenoptera, 15 other Hymenoptera, 3 species of Coccidae, and 70 Orthoptera ; from Bulgaria.

Mr. R. W. E. Tucker, Government Entomologist :—4 Diptera, 50 Parasitic Hymenoptera, and 15 Lepidoptera ; from the Barbados.

Mr. G. C. Ullyett : —23 Diptera and 6 cocoons, and 50 Parasitic Hymenoptera ; from South Africa.

U.S. National Museum, Washington : -34 Braconidae : from the United States of America.

Wellcome Tropical Research Laboratories, Khartoum : —400 Parasitic Hymenoptera ; from the Sudan.

Mr. P. Zangheri :—23 Parasitic Hymenoptera ; from Italy.

GENERAL INDEX.

A.

Abbella tomaspidis, sp. n., parasite of *Tomaspis saccharina*, in Trinidad, **206.**
abdominalis, Rhembobius (*Phygadeuon*).
abnormalis, Aëdes.
abruptus, Thyridanthrax.
Acacia, locusts feeding on, **54–56, 62.**
Acanthacris ruficornis, effect of crowding on, in S. Africa, **403.**
Achillea millefolium, food-plant of *Smynthurus viridis* in England, **103.**
Acridium aeruginosum (see *Cyrtacanthacris tatarica*).
Acridium coangustatum (see *Nomadacris septemfasciata* ph. *solitaria*).
Aëdes abnormalis, **562.**
Aëdes (*Finlaya*) *albitarsis*, **76, 77.**
Aëdes (*Stegomyia*) *albopictus*, malformation in male hypopygium of, **233.**
Aëdes alboventralis, **562.**
Aëdes (*Ochlerotatus*) *annulipes*, **229.**
Aëdes (*Finlaya*) *argenteitarsis*, sp. n., from New Guinea, **76.**
Aëdes (*Stegomyia*) *argenteus* (*fasciata*), analysis of breeding-places of, in Trinidad, **492–494 ;** *Megarhinus kempi* predacious on, **73 ;** chitinisation of larvae of *Filaria repens* in, **229 ;** methods of rearing, **29.**
Aëdes cinereus, **229.**
Aëdes (*Finlaya*) *derooki*, sp. n., from Moluccas, **75.**
Aëdes durbanensis, **562.**
Aëdes (*A.*) *dux*, hypopygium of, **79.**
Aëdes eatoni, in Madeira, **560.**
Aëdes (*Stegomyia*) *fasciatus* (see *A. argenteus*).
Aëdes funereus, hypopygium of, **79.**
Aëdes (*Skusea*) *iyengari*, larva of, **78.**
Aëdes (*Aëdimorphus*) *leesoni*, sp. n., from S. Rhodesia, **562.**
Aëdes macrodixoa, hypopygium of, **79.**
Aëdes (*Leptosomatomyia*) *medialis*, sp. n., from New Guinea, **79.**
Aëdes (*Aëdimorphus*) *natronius*, sp. n., from Uganda, **562.**
Aëdes (*Ochlerotatus*) *purpuraceus*, sp. n., from New Guinea, **77.**
Aëdes rhecter, **562.**
Aëdes scapularis, in Trinidad, **495.**
Aëdes (*Stegomyia*) *variegatus*, **492**]; chitinisation of larvae of *Filaria bancrofti* in, **229.**
Aëdimorphus (see *Aëdes*).
aegyptiacus, Sphex.
aegyptium, Anacridium.
aenos, Stomoxys (see *S. calcitrans*).
aequalis, Euaresta.
aeruginosum, Acridium (see *Cyrtacanthacris tatarica*).
Africa, South, phases of locusts in, **293–405.**
africanum, Lecanium.
albimanus, Anopheles.
albitarsis, Aëdes (*Finlaya*).
albopictus, Aëdes (*Stegomyia*).
alboventralis, Aëdes.
Almond, control of *Cerambyx dux* on, in Palestine, **251.**
Alopecurus pratensis, influence of percentage of, on *Smynthurus viridis*, **173.**
Alysia manducator, value of, as a parasite of *Lucilia sericata*, **241–245 ;** reproductive capacity of, **241.**
Amaryllis, food-plant of *Merodon equestris*, **431.**
ambiguella, Clysia.
amenocles, Chalcis.
America, South, morphology of *Phlebotomus* spp. of, **17–23.**
amygdali, Scolytus.
Anacridium aegyptium, distribution of, **49.**
Anacridium arabicum, in Arabia, **49.**
Anacridium flavescens, in India, **49.**
Anacridium moestum (Tree Locust), distribution and phases of, in Sudan, **49–51.**
Anacridium moestum melanorhodon, bionomics of, in Sudan, **54–58 ;** description of stages of, **51–53.**
Anagrus spp., parasites of leafhoppers in Sweden & U.S.A., **42.**
Anagrus armatus, **206.**
Anagrus flaveolus, **206.**
Anagrus urichi, sp. n., parasite of *Tomaspis saccharina* in Trinidad, **204 ;** life-history of, **207–208**
Anastatus bifasciatus, parasite of *Antestia lineaticollis* in Kenya, **217.**

Anatolia, Western, ecological studies on *Dociostaurus maroccanus* in, **273–287.**
andersoni, Culex.
Andrena, **116.**
Andropogon spp., food-plants of *Diatraea saccharalis* in tropical America, **267, 268.**
Anguillulina dipsaci (Bulb Eelworm), **430, 432, 443.**
angulifera, Kraussaria.
annulatus, Taeniorhynchus (*Mansonioides*).
annulipes, Aëdes (*Ochlerotatus*) ; *Taeniorhynchus* (*Mansonioides*).
Anopheles, **229.**
Anopheles albimanus, in Trinidad, **494.**
Anopheles apicimacula, in Trinidad, **494.**
Anopheles argyritarsis, in Trinidad, **494.**
Anopheles bellator, in Trinidad, **494.**
Anopheles eiseni, in Trinidad, **494.**
Anopheles elutus, determination of age of, by size of common oviduct, **563–566.**
Anopheles maculipennis, **492.**
Anopheles tarsimaculatus, analysis of breeding-places of, in Trinidad, **479–492.**
antennatis, Calliphora.
Antestia, **94, 96, 98.**
Antestia lineaticollis, life-history and control of, on coffee in Kenya, **217–228.**
antestiae, Hadronotus.
Anthocoris nemorum, predacious on *Smynthurus viridis,* **122.**
anthomyiarum, Figites.
Antilles, food-plants of *Diatraea* spp. in, **259–260.**
antipodea, Calliphora.
Anuraphis padi (*helichrysi*), on potato in Br. Isles, **546.**
Anurida maritima, **104.**
Apanteles coffea, parasite of *Thliptoceras* in Kenya, **223.**
Aphids, ecological studies of, on potato in Br. Isles, **535–548.**
Aphis solanina, on potato, **535.**
Aphis sorghi, Coccinellid predacious on, in Sudan, **119.**
apicimacula, Anopheles.
Apricot, control of *Cerambyx dux* on, in Palestine, **251.**
Aprostocetus, parasite of *Antestia lineaticollis* in Kenya, **217.**
arabicum, Anacridium.
aranoides, Rachionotomyia.
araozi, Phlebotomus.
argenteitarsis, Aëdes (*Finlaya*).
argenteus, Aëdes.
argentifrons, Thyridanthrax.
argyritarsis, Anopheles.
armatus, Anagrus.
Arrhenatherum avenaceum, influence of percentage of, on *Smynthurus viridis,* **173.**
Asparagus sprengeri, food-plant of *Erythroneura parvula,* **42.**
astia, Xenopsylla.
asullepta, Limatus.
atlantica, Theobaldia.
augur, Calliphora.
aurantii, Toxoptera.
aurea, Heizmannia.
aureopunctata, Calliphora (see *C. hortona*).
auricularia, Forficula.
aurifluus, Megarhinus.
auriventris, Calliphora.
auronotata, Calliphora.
Australia, revision of *Calliphora,* subgenera *Neopollenia* and *Proekon,* in, **549–558 ;** oviposition stimuli of *Euaresta aequalis* in, **191–193 ;** *Sarcophaga peregrina* and allied spp. in, **45–48;** distribution of *Smynthurus viridis* in, **182.**
australis, Calliphora.
autumnalis, Leptus ; Musca (see *M. corvina*).
Axonopus capillaris, food-plant of *Diatraea saccharalis* in tropical America, **268.**
Azadirachta indica, not attacked by locusts in Sudan, **63.**
Azores, new mosquito from, **561.**
azoriensis, Culex (see *C. pipiens*).

B.

Baits, for locusts, **450–459.**
Balanites aegyptiaca, locust feeding on, **56.**
bancrofti, Filaria.
Barycornus, parasite of *Antestia lineaticollis* in Kenya, **217.**
Batrachotettix spp., in S. Africa, **320.**
Beetroot (*Beta vulgaris*), attempts to feed locusts on, **360.**
bellator, Anopheles.
bellifactella, Diatraea.
Bembidium lampros, predacious on *Longitarsus parvulus,* **120.**
Bembidium littorale, predacious on *Smynthurus viridis,* **120.**
Bembidium mutatum, predacious on *Chortophila brassicae,* **120.**
Beta vulgaris (see Beetroot).
bezzii, Calliphora.
bifasciatus, Anastatus.
Birds, attacking locusts in Sudan, **57.**

bodkini, Tomaspis.
Bombus, **116.**
botrana, Polychrosis.
Brassica napus (see Swede).
Brassica oleracea (see Cabbage).
brassicae, Chortophila.
brevicornis, Mormoniella.
brevipalpus, Culex.
briggsi, Ectopsocus.
British Isles, ecological studies of Aphids on potato in, **535–548**; super-parasitism of *Collyria calcitrator* in, **211–216**; biology of *Erythroneura* spp. in, **33–43**; comparison of *Eumerus* spp. infesting narcissus in, **247–249**; natural control of *Lucilia sericata* in, **235–245**; bionomics and control of *Merodon equestris* in, **429–448**; bionomics of sawflies infesting *Ribes* in, **1–15**; ecological study of *Smynthurus viridis* in, **101–145, 151–190.**
bromeliarum, Wyeomyia.
brucei, Trypanosoma.
brunnipes, Lathrobium.
Bulb Eelworm (see *Anguillulina dipsaci*).
bulborum, Merodon equestris.
Burr Seed Fly (see *Euaresta aequalis*).
buscklla, Diatraea.

C.

Cabbage (*Brassica oleracea*), food-plant of *Myzus persicae* in Br. Isles, **546.**
Cadaba rotundifolia, locust on, **54.**
caesar, Lucilia.
Cage, for rearing mosquitos, **29.**
Calceolaria, food-plant of *Erythroneura parvula*, **42.**
calcitrans, Stomoxys.
calcitrator, Collyria.
Calcium Cyanide, fumigation with, against *Merodon equestris*, **444.**
caliginea, Glossina.
Calliphora, **48**; (*Neopollenia*) Australian spp. of (key **550**), **549–553**; (*Proekon*), Australian spp. of (key **554**), **554–558**; relation of, to *Lucilia sericata*, **240, 244.**
Calliphora antennatis, in New Zealand, **475.**
Calliphora antipodea, in sub-antarctic islands, **475.**
Calliphora augur, in Australia, **555.**
Calliphora aureopunctata (see *C. hortona*).
Calliphora auriventris, in Australia, **549.**
Calliphora auronotata, in New Zealand, **473–474.**
Calliphora australis, in Australia, **551.**
Calliphora bezzii, sp. n., from Australia, **551.**
Calliphora canimicans, in Australia, **549.**
Calliphora centralis, in Australia, **557.**
Calliphora cockaynei (see *C. quadrimaculata*).
Calliphora dasyophthalma, in New Zealand, **473, 474.**
Calliphora deflexa, sp. n., from Australia, **552.**
Calliphora erythrocephala, in New Zealand, **475.**
Calliphora eudypti, in sub-antarctic islands, **475.**
Calliphora falciformis, sp. n., from Australia, **558.**
Calliphora fallax, in Australia, **549.**
Calliphora fulvicoxa, in Australia, **551.**
Calliphora fuscofemorata, **554, 558.**
Calliphora hilli, in Australia, **549**; in New Zealand, **470, 472, 473, 475.**
Calliphora hortona (*Musca icela*), in New Zealand, **473, 474.**
Calliphora macleayi, **554, 558.**
Calliphora nociva, sp. n., from Australia, **556.**
Calliphora oceaniae, distinct from *C. augur*, **555.**
Calliphora quadrimaculata, in New Zealand, **471, 473–475.**
Calliphora rufipes, in Australia, **549, 553.**
Calliphora sternalis, in Australia, **553.**
Calliphora stygia, in Australia, **550**; in New Zealand, **470, 472–474.**
Calliphora tessellata, Bezzi nec Macq. (see *C. bezzii*).
Calliphora tibialis, in Australia, **549.**
Calliphora violacea, in New Zealand, **475.**
Calliphoridae, historical review of, in New Zealand, **469–476.**
Calliptamus, **279.**
cancer, Deinocerites.
candidipes, Uranotaenia.
canella, Diatraea.
canimicans, Calliphora.
Canna, attempts to feed locusts on, **360.**
Cape Weed (see *Cryptostemma calendulaceum*).
capito, Locusta migratoria.
Carbon Bisulphide, against *Cerambyx dux* in Palestine, **253**; fumigation with, against *Merodon equestris*, **444.**
Carpophilus, **195.**
Castnia licoides, original habitat of, in tropical America, **268–270.**
castrensis, Culex.

Cattle, trypanosomes in, in the Gold Coast, **502.**
Centaurea nigra, food-plant of *Smynthurus viridis* in England, **103.**
centralis, Calliphora.
cephalus, Xantholinus.
Cephus pygmaeus, super-parasitism of, by *Collyria calcitrator* in England, **211–216.**
Cerambyx dux, bionomics and control of, on stone-fruit trees in Palestine, **251–256 ;** methods of rearing, **254.**
Ceratophyllus fasciatus, methods of rearing, **25, 27.**
Ceratophyllus wickhami, methods of rearing, **25.**
Cerococcus hibisci, effect of bait sprays on natural enemies of, in Kenya, **226.**
Ceroplastes destructor, **224 ;** effect of bait sprays on natural enemies of, in Kenya, **226.**
Ceroplastes rubens, effect of bait sprays on natural enemies of, in Kenya, **226.**
Chaetochlora sulcata, original food-plant of *Diatraea bellifactella* in tropical America, **262, 267, 268.**
Chalarus, **116.**
Chalcis amenocles, parasite of *Glossina* spp., **463.**
Chenopodium album (see Goosefoot).
cheopis, Xenopsylla.
Chickweed (*Stellaria media*), food-plant of *Myzus persicae* in Br. Isles, **546.**
Chortophila brassicae, predacious enemies of, **120.**
Chrysanthemum, food-plant of *Anuraphis padi*, **546 ;** food-plant of *Erythroneura* spp., **42.**
Chrysomyia, relations of, to *Lucilia sericata*, **240, 244.**
Chrysomyia megacephala, in New Zealand, **475.**
cicindeloides, Stenus.
cinereus, Aëdes.
cingulata, Psorophora.
cingulatus, Paederus.
circumflexus, Myzus.
Clysia ambiguella, Coccinellid predacious on, in France, **118.**
coangustatum, Acridium (see *Nomadacris septemfasciata* ph. *solitaria*).
Coccinella septempunctata, predacious on *Smynthurus viridis*, **118, 125, 184.**
Coccinella undecimpunctata, predacious on *Smynthurus viridis*, **119.**
cockaynei, Calliphora (see *C. quadrimaculata*).
Coelalysia glossinophaga, parasite of *Glossina morsitans*, **463.**
coerulescens, Oedipoda.
coffea, Apanteles.
coffeae, Diarthrothrips.
Coffee, control of *Antestia lineaticollis* on, in Kenya, **217–228 ;** bionomics and control of *Lygus simonyi* on, in Kenya, **85–99.**
Coffee Berry Borer Moth (see *Thliptoceras octoguttalis*).
Coffee Leaf Miner Moth (see *Leucoptera coffeella*).
coffeella, Leucoptera.
Coix lachryma-jobi, food-plant of *Diatraea saccharalis* in tropical America, **268.**
Collyria calcitrator, super-parasitism by, **211–216.**
congolense, Trypanosoma.
Conopomyia hybrida (see *Ficalbia*).
Coreopsis, attempts to feed locusts on, **360.**
corniger, Culex.
coronator, Culex.
cortelezzii, Phlebotomus.
corvina, Musca.
coryli, Nematospora.
Cotton, locust feeding on, **56.**
cristatus, Xysticus.
cruciatus, Phlebotomus.
Cryptostemma calendulaceum (Cape Weed), food-plant of *Smynthurus viridis* in Australia, **103.**
Culex andersoni, **562.**
Culex azoriensis (see *C. pipiens*).
Culex brevipalpus, Megarhinus kempi predacious on, **73.**
Culex castrensis var. *foliatus*, n., from Java, **82.**
Culex corniger, in Trinidad, **495.**
Culex coronator, in Trinidad, **495.**
Culex (*Lophoceratomyia*) *digoelensis*, sp. n., from New Guinea, **81.**
Culex fatigans, in Trinidad, **495.**
Culex hancocki, **562.**
Culex hopkinsi, sp. n., from Uganda, **562.**
Culex (*Lophoceratomyia*) *infantulus*, **82.**
Culex musarum, sp. n., from Uganda, **562.**
Culex papuensis, hypopygium of, **82.**
Culex pipiens, in Azores, **560 ;** cysts of *Proteosoma* in, **229.**
Culex scotti, in Seychelles, **562.**
Culex squamosus, hypopygium of, **82.**
Culex varioannulatus (see *C. pipiens*).
Cutworm, Pale Western (see *Porosagrotis orthogonia*).
cyanea, Ornithacris.
cyaneus, Sabethes.
cyanipennis, Cyrtosus.
Cynodon dactylon, relation of breeding-places of *Dociostaurus maroccanus* to, in Western Anatolia, **279.**
Cynometra vogelii, relation of *Glossina* to, in the Gold Coast, **506, 519–524.**

Cyperus, locust larvae feeding on, **56.**
Cyrtacanthacris tatarica (*ranacea*) (Brown-spotted Locust), morphology and biology of, in Sudan, **59–64.**
Cyrtosus cyanipennis, predacious on *Smynthurus viridis*, **120, 125, 184.**

D.

Dactylis glomeratus, influence of percentage of, on *Smynthurus viridis*, **173.**
Daphne, food-plant of *Myzus persicae*, **546.**
dasyophthalma, Calliphora.
Datura stramonium, Euaresta aequalis not ovipositing on, **192.**
decemlineata, Leptinotarsa.
deflexa, Calliphora.
degeerii, Pachygnatha.
Deinocerites cancer, in Trinidad, **495.**
demissum, Sepimentum.
dentata, Trachygnatha.
dentipes, Hydrotaea.
depressum, Stirastoma.
derooki, Aëdes (*Finlaya*).
destructor, Ceroplastes.
Diarthrothrips coffeae, **225.**
Diatraea bellifactella, food-plants of, in tropical America, **259–268.**
Diatraea busckella, food-plants of, in tropical America, **259–268.**
Diatraea canella, food-plants of, in tropical America, **259–268.**
Diatraea impersonatella, food-plants of, in tropical America, **259–268.**
Diatraea lineolata, confined to maize, **259.**
Diatraea saccharalis, food-plants of, in tropical America, **259–268.**
diatraeae, Lixophaga.
digitata, Joblotia.
digoelensis, Culex (*Lophoceratomyia*).
dipsaci, Anguillulina.
Dirhinus inflexus, parasite of *Glossina morsitans*, **463.**
Dociostaurus maroccanus, ecological studies of, in Western Anatolia, **273–287.**
domestica, Musca.
durbanensis, Aëdes.
durhami, Limatus.
dux, Aëdes ; *Cerambyx.*

E.

eatoni, Aëdes.
Echinochloa polystachya, original food-plant of *Diatraea saccharalis* in tropical America, **263, 268.**
Ectopsocus briggsi, predacious on mealybugs in Kenya, **224, 225.**
eiseni, Anopheles.
Eleusine indica, food-plant of *Diatraea saccharalis* in tropical America, **266, 268.**
elutus, Anopheles.
Epeira umbratica, predacious on *Smynthurus viridis*, **124.**
Epineura rubens, parasite of *Antestia* in Kenya, **225.**
equestris, Merodon.
Erigone spp., predacious on *Smynthurus viridis*, **123, 125, 184.**
erythrocephala, Calliphora.
Erythroneura pallidifrons, morphology and biology of, in Br. Isles, **33–43.**
Erythroneura parvula, morphology and biology of, in Br. Isles, **33–43.**
Euaresta aequalis, oviposition stimuli of, in Australia, **191–193.**
Euchlaena mexicana (Teosinte), a possible food-plant of *Diatraea lineolata*, **259.**
Eucosma nereidopa, **224.**
eudypti, Calliphora.
Eumerus spp., **430, 435, 442.**
Eumerus strigatus, larva of, compared with *E. tuberculatus*, **247.**
Eumerus tuberculatus, larva of, **248.**
Eurycles, food-plant of *Merodon equestris*, **431.**
Evophrys, predacious on *Smynthurus viridis*, **124, 126.**

F.

faber, Melamphaus.
falciformis, Calliphora.
fallax, Calliphora.
fasciatus, Aëdes (*Stegomyia*) (see *A. argenteus*) ; *Ceratophyllus.*
fatigans, Culex.
Federated Malay States, bionomics of *Melamphaus faber* in, **195–201.**
ferox, Psorophora.
Festuca ovina, influence of percentage of, on *Smynthurus viridis*, **173.**
Ficalbia (*Mimomyia*) *hispida*, **561.**
Ficalbia (*Mimomyia*) *hybrida*, morphology of, in Netherlands Indies, **69–72.**
Ficalbia (*Mimomyia*) *perplexens*, sp. n., from Uganda, **561.**
Ficus, locust feeding on, **56, 63.**
Figites anthomyiarum, parasite of *Lucilia sericata*, **244.**
Filaria spp., chitinisation of larva of, in mosquitos, **229.**
Finlaya, a subgenus of *Aëdes*, q.v.
flaveolus, Anagrus.

flavescens, Anacridium.
flaviventris, Schistocerca gregaria.
Fleas, methods of collecting and rearing, **25–29.**
foliatus, Culex castrensis.
Forficula auricularia, predacious on *Smynthurus viridis*, **122, 123, 183.**
froggatti, Sarcophaga.
frontalis, Sarcophaga.
frontosa, Goeldia.
Fuchsia, food-plant of *Erythroneura* spp., **42.**
fulvicoxa, Calliphora.
fumosum, Sepimentum.
funereus, Aëdes.
fusca, Glossina.
fuscicauda, Sarcophaga.
fuscipes, Otiorrhynchus.
fuscofemoratus, Calliphora.

G.

Galanthus, food-plant of *Merodon equestris*, **431.**
Galtonia, food-plant of *Merodon equestris*, **431.**
gei, Macrosiphum.
Geocoris ruficeps, predacious on *Lygus simonyi*, **92.**
Geoica (*Tychea*) *phaseoli*, on potato, **535.**
geometrica, Uranotaenia.
Geranium, food-plant of *Erythroneura* spp., **42.**
giraulti, Oligosita.
Glossina spp., ecological relations of, in the Gold Coast, **519–531 ;** pupal parasites of, in Nigeria, **463–467 ;** clearing against, **507–513, 526–530 ;** relation of, to game, **505–507, 516–517, 524.**
glossinae, Mutilla ; Syntomosphyrum.
glossinophaga, Coelalysia.
Goeldia frontosa, in Trinidad, **495.**
Gold Coast, bionomics and control of *Glossina* spp. in, **501–531.**
Gonocephalum, **223.**
Goosefoot (*Chenopodium album*), food-plant of *Myzus persicae* in Br. Isles, **546.**
Gossypium, food-plant of *Erythroneura* spp., **42.**
gracilis, Oedaleus (see *O. nigrofasciatus*).
gregaria, Schistocerca.
Guiana, British, food-plants of sugar-cane pests in, **263, 269–270.**
Guiana, Dutch, food-plants of *Diatraea* spp. in, **263.**

H.

Habranthus, food-plant of *Merodon equestris*, **431.**
Hadronotus antestiae, parasite of *Antestia lineaticollis* in Kenya, **217.**
Haemagogus spp., in Trinidad, **495.**
hamata, Singa.
hamatus, Xantholinus.
hampei, Stephanoderes.
hancocki, Culex.
Heizmannia aurea, sp. n., from Moluccas, **75.**
helichrysi, Anuraphis (see *A. padi*).
Heliconia spp., food-plants of *Castnia licoides* in tropical America, **269–270.**
hesperidum, Lecanium.
hibisci, Cerococcus.
hilli, Calliphora.
hispida, Ficalbia (*Mimomyia*).
Hong Kong, larva of *Uranotaenia testacea* in, **559.**
hopkinsi, Culex ; Uranotaenia.
hortona, Calliphora.
Humidity, effect of, on development of *Smynthurus viridis*, **135–138, 142, 157–168.**
hutsoni, Sarcophaga.
Hyacinth, food-plant of *Merodon equestris*, **431.**
hybrida, Ficalbia (*Mimomyia*).
Hydnocarpus spp., *Melamphaus faber* on, in F.M.S., **195.**
Hydrogen Ion Concentration, effect of, on development of *Smynthurus viridis*, **132–135, 138–140, 143, 168–172 ;** relation of, to mosquito larvae in Trinidad, **482.**
Hydrotaea dentipes, predacious on blow-flies, **244.**
Hymenachne spp., original food-plants of *Diatraea saccharalis* in tropical America, **260, 261, 263, 265, 268.**
Hypera, **174.**

I.

icela, Calliphora (*Musca*) (see *C. hortona*).
Icerya nigroareolata, effect of bait sprays on natural enemies of, in Kenya, **226.**
Idia murina, not occurring in New Zealand, **474, 475.**
immitis, Filaria.
impersonatella, Diatraea.
infantulus, Culex (*Lophoceratomyia*).
inflexus, Dirhinus.
intermedius, Phlebotomus.

Ips pini, Staphylinid predacious on, **120.**
Iris, Eumerus strigatus on, **247.**
irrequieta, Sarcophaga.
Isotoma macnamarai, **104.**
Isotoma sepulchralis, **104.**
Isotoma viridis, **175.**
iyengari, Aëdes (*Skusea*).

J.

Joblotia digitata, in Trinidad, **495.**

K.

karnyi, Sarcophaga.
kempi, Megarhinus.
Kenya Colony, control of *Antestia lineaticollis* in, **217–228 ;** bionomics and control of *Lygus simonyi* on coffee in, **85–99.**
Kleidotoma marshalli, parasite of *Lucilia sericata*, **244.**
Kraussaria angulifera, egg-stage of, **62.**

L.

lacmica, Musca (see *Calliphora stygia*).
laminatus, Philonthus.
lampros, Bembidium.
lateralis, Ochromyia (see *Calliphora augur*).
Lathrobium brunnipes, predacious on *Smynthurus viridis*, **119, 125, 184.**
Lathyrus pratensis, influence of percentage of, on *Smynthurus viridis*, **173.**
Lecanium spp., effect of bait sprays on natural enemies of, in Kenya, **226.**
leesoni, Aëdes (*Aëdimorphus*).
leicesteri, Megarhinus.
Lephthyphantes zimmermannii, predacious on *Smynthurus viridis*, **123, 125, 184.**
Leptinotarsa decemlineata, **132.**
Leptochloa spp., food-plants of *Diatraea saccharalis* in tropical America, **268.**
Leptosomatomyia (see *Aëdes*).
Leptus autumnalis, **229.**
Leucojum, food-plant of *Merodon equestris*, **431.**
Leucoptera coffeella (Coffee Leaf Miner Moth), on coffee in Kenya, **226.**
leucotrochus, Pteronidea.
licoides, Castnia.
Ligustrum vulgare, attempts to feed locusts on, **360.**
lilacinus, Pseudococcus.
Limatus asullepta, in Trinidad, **495.**
Limatus durhami, in Trinidad, **495.**
linearis, Xantholinus.
lineata, Psorophora.
lineaticollis, Antestia.
lineolata, Diatraea.
littorale, Bembidium.
littoralis, Paederus.
Lixophaga diatraeae, parasite of *Diatraea saccharalis* in Antilles & Haiti, **259, 260.**
Locusta migratoria, **51, 58.**
Locusta migratoria capito, in Madagascar, **309.**
Locusta migratoria migratorioides, distribution and phases of, in S. Africa, **339–363 ;** sodium fluosilicate against hoppers of, in Nigeria, **449–461 ;** experiments with poison dusts against, in Sudan, **65–68 ;** causes of development of *gregaria* characters in, **364–385.**
Locustana pardalina, phases of, in S. Africa, **301–335 ;** distribution and breeding-grounds of, **387–392 ;** effect of temperature on, **376 ;** embryonic diapause of, **393–398 ;** albino race of, **398–401.**
Locusts, ecology of, in W. Anatolia, **273–287 ;** phases of, in S. Africa, **293–405.**
Locust, Brown-spotted (see *Cyrtacanthacris tatarica*).
Locust, Desert (see *Schistocerca gregaria*).
Locust, Moroccan (see *Dociostaurus maroccanus*).
Locust, Tree (see *Anacridium moestum*).
longipalpis, Glossina.
Longitarsus melanocephalus, effect of temperature on survival of, **165.**
Longitarsus parvulus, Carabid predacious on, **120.**
Lophoceratomyia (see *Culex*).
lowii, Uranotaenia.
Lucerne Flea (see *Smynthurus viridis*).
Lucilia, **48.**
Lucilia caesar, not occurring in New Zealand, **475** (note).
Lucilia sericata, natural control of, in England, **235–245 ;** in New Zealand, **475 ;** reproductive capacity of, **237.**
Ludlowia minima (see *Ficalbia hybrida*).
Luziola spruceana, original food-plant of *Diatraea saccharalis* in tropical America, **260, 268.**
Lycidocoris mimeticus, on coffee in E. Africa, **95.**
Lygus pabulinus, **96.**
Lygus pratensis, predacious on *Smynthurus viridis*, **122.**
Lygus simonyi, on coffee in Kenya, **85–99, 224–225 ;** bionomics and control of, **85–99.**

M.

macckrackenae, Theobaldia.
macfarlanei, Uranotaenia.
macleayi, Calliphora.
macnamarai, Isotoma.
macrodixoa, Aëdes.
Macrosiphum gei, ecological studies of, on potato in Br. Isles, **535–547.**
maculipennis, Anopheles.
Madeira, *Aëdes eatoni* in, **560.**
magnifica, Scintharista.
maidis, Peregrinus.
Maize, *Diatraea lineolata* on, **259.**
malayi, Microfilaria.
manducator, Alysia.
Mansonioides (see *Taeniorhynchus*).
maritima, Anurida.
maroccanus, Dociostaurus.
marshalli, Kleidotoma.
mazzai, Phlebotomus (see *P. intermedius*).
medialis, Aëdes (*Leptosomatomyia*).
medicorum, Glossina.
megacephala, Chrysomyia.
Megarhinus aurifluus, biology of, in Sumatra, **73.**
Megarhinus kempi, biology of, in Java, **73.**
Megarhinus leicesteri, **73.**
Megarhinus quasiferox, **73.**
Megarhinus superbus, in Trinidad, **495.**
Megarhinus trichopygus, in Trinidad, **495.**
Megarhinus trinidadensis, in Trinidad, **495.**
Melamphaus faber, bionomics of, in F.M.S., **195–198 ;** developmental stages of, **198–201.**
melanocephalus, Longitarsus.
melanorhodon, Anacridium moestum.
Merodon equestris (Large Narcissus Fly), morphology and biology of, in Br. Isles, **429–441 ;** control of, **441–447 ;** varieties of, **434.**
Mesembryanthemum, visited by *Merodon equestris*, **435.**
Meta segmentata, predacious on *Smynthurus viridis*, **123, 126.**
Meteorological Conditions, influence of, on locusts in W. Anatolia, **279–287.**
micans, Stomatoceras.
Microdus, **264, 267.**
Microdus stigmaterus, parasite of *Diatraea saccharalis* in Haiti, **260.**
Microfilaria malayi, chitinisation of larvae of, in mosquitos, **230.**
migonei, Phlebotomus.
migratoria, Locusta.
migratorioides, Locusta migratoria.
mimeticus, Lycidocoris.
Mimomyia (see *Ficalbia*).
minima, Ludlowia (see *Ficalbia hybrida*).
misera, Sarcophaga.
moestum, Anacridium.
Moluccas, new mosquitos from, **75, 76.**
Mormoniella brevicornis, parasite of *Lucilia sericata*, **244.**
morsitans, Glossina.
Mosquitos, larvae of, in Netherlands Indies, **73–83 ;** physico-chemical factors of water in relation to breeding of, in Trinidad, **477–496 ;** list of, in Trinidad, **494–495 ;** determination of age of, by size of common oviduct, **563–566 ;** chitinisation of parasites in, **229–231 ;** methods of rearing, **29–31.**
murina, Idia.
musarum, Culex.
Musca corvina (*autumnalis*), in New Zealand, **475.**
Musca domestica, in New Zealand, **473–475.**
Musca laemica (see *Calliphora stygia*).
Musca taitensis, in New Zealand, **473–474.**
Musca vicaria (see *M. domestica*).
Muscidae, historical review of, in New Zealand, **469–476.**
mutatum, Bembidium.
Mutilla glossinae, parasite of *Glossina morsitans*, **463.**
Myosotis, food-plant of *Anuraphis padi*, **546.**
Myzus circumflexus, on potato, **535.**
Myzus persicae, ecological studies of, on potato in Br. Isles, **535–547.**
Myzus pseudosolani, ecological studies of, on potato in Br. Isles, **535–547.**

N.

narcissi, Merodon equestris.
Narcissus, bionomics and control of Syrphids on, in Br. Isles, **247, 429–448.**
Narcissus Fly, Large (see *Merodon equestris*).
natronius, Aëdes (*Aëdimorphus*).
Nectarine, food-plant of *Myzus persicae*, **546.**
neivai, Phlebotomus (see *P. intermedius*).
Nematospora coryli, infesting coffee in Tanganyika, **217** (note).
nemorum, Anthocoris.
Neopollenia, a subgenus of *Calliphora*, q.v.
nereidopa, Eucosma.
Netherlands Indies, mosquitos from, **69–83.**

New Guinea, new mosquitos from, **76, 78, 81, 82.**
New Zealand, historical review of Muscidae and Calliphoridae of, **469–476.**
Nicotiana, food-plant of *Erythroneura* spp., **42.**
Nicotine Sulphate, in formula against *Antestia*, **218.**
Nigeria, measures against *Locusta migratoria migratorioides* in, **449–461.**
Nigeria, Northern, pupal parasitism of *Glossina* spp. in, **463–467.**
nigra, Saissetia ; Salpingogaster.
nigricornis, Ochromyia (see *Calliphora augur*).
nigroareolata, Icerya.
nigrofasciatus, Oedaleus.
nigrofusca, Glossina.
nociva, Calliphora.
Nomadacris septemfasciata, **59 ;** phases of, in S. Africa, **335–339.**
Nosema, **229.**
nubilalis, Pyrausta.

O.

Oak, Valonia (see *Quercus aegilops*).
oblongus, Tibellus.
obscurus, Volumnus.
oceaniae, Calliphora.
Ochlerotatus, a subgenus of *Aëdes*, q.v.
Ochromyia (see *Calliphora*).
octoguttalis, Thliptoceras.
Oedaleus nigrofasciatus (*gracilis*), in S. Africa, **391 ;** effect of crowding on, **402–403.**
Oedipoda coerulescens, **321.**
oleae, Saissetia.
*Oligosita girault*i, parasite of *Tomaspis saccharina* in Trinidad, **208.**
Olives, relation of breeding-places of *Dociostaurus maroccanus* to, in W. Anatolia, **277.**
Onion, *Eumerus strigatus* on, **247.**
Ornithacris cyanea, **336.**
orthogonia, Porosagrotis.
Oryza latifolia, original food-plant of *Diatraea saccharalis* in tropical America, **267, 268.**
Otiorrhynchus fuscipes, **230.**

P.

pabulinus, Lygus.
Pachira aquatica, original food-plant of *Stirastoma depressum*, **264.**
Pachygnatha degeerii, predacious on *Smynthurus viridis*, **124, 125, 184.**
padi, Anuraphis.
Paederus cingulatus, predacious on *Smynthurus viridis* in S. Australia, **184.**
Paederus littoralis, predacious on *Smynthurus viridis*, **120, 125, 183, 184.**
paganus, Stenus.
Palestine, bionomics and control of *Cerambyx dux* in, **251–256.**
pallicera, Glossina.
pallidifrons, Erythroneura.
pallipes, Pristiphora.
palpalis, Glossina.
Panicum, locust larvae feeding on, **56 ;** food-plant of *Diatraea* spp. in tropical America, **260–261, 264–268.**
papatasii, Phlebotomus.
papuensis, Culex.
Paradichlorbenzene, fumigation with, against *Merodon equestris*, **443.**
Paraffin, and pyrethrum against *Lygus simonyi*, **96–99.**
pardalina, Locustana.
Paris Green, in poison bait formula against *Antestia*, **219.**
Parsnip, *Eumerus strigatus* on, **247.**
parvula, Erythroneura.
parvulus, Longitarsus.
Paspalum spp., food-plants of *Diatraea* spp. in tropical America, **259–268.**
Paspalum virgatum, Castnia licoides on, in Trinidad, **270.**
Peach, control of *Cerambyx dux* on, in Palestine, **251 ;** food-plant of *Myzus persicae*, **546.**
peregrina, Sarcophaga.
Peregrinus maidis, **206.**
Perilampus violaceus, parasite of *Glossina morsitans* in Nigeria, **466.**
perplexens, Ficalbia (*Mimomyia*).
persicae, Myzus.
phaseoli, Geoica (*Tychea*).
Philodromus, predacious on *Smynthurus viridis*, **122, 125, 184.**
Philonthus laminatus, predacious on *Smynthurus viridis*, **119, 126.**
Philonthus politus, predacious on *Smynthurus viridis*, **119, 126.**
Phlebotomus araozi, distinct from *P. migonei*, **21.**
Phlebotomus cortelezzii, morphology of, **21.**
Phlebotomus cruciatus, **23.**
Phlebotomus intermedius (*mazzai*), morphology of, **18.**
Phlebotomus migonei, morphology of, **19.**
Phlebotomus neivai (see *P. intermedius*).
Phlebotomus papatasii, **19.**
Phlebotomus trinidadensis, morphology of, **22.**

Phlebotomus verrucarum, **23.**
Phygadeuon abdominalis (see *Rhembobius*).
pini, Ips.
pipiens, Culex.
Pistia, mosquitos breeding amongst, **69, 72.**
Pithecolobium dulce, locust larvae feeding on, **56.**
Plantago bellardi, relation of breeding-places of *Dociostaurus maroccanus* to, in W. Anatolia, **278.**
Ploiariodes, **224.**
Poa pratensis, influence of percentage of, on *Smynthurus viridis*, **173.**
politus, Philonthus.
Pollenia rufipes, **553.**
Polychrosis botrana, Coccinellid predacious on, in France, **118.**
Porosagrotis orthogonia (Pale Western Cutworm), **177.**
Potato, ecological studies of Aphids on, in Br. Isles, **535–548.**
pratensis, Lygus.
Primula, food-plant of *Erythroneura* spp., **42.**
Pristiphora pallipes, bionomics of, on *Ribes* in Br. Isles, **10–15.**
Proekon, a subgenus of *Calliphora*, q.v.
Proteosoma, cysts of, in *Culex pipiens*, **229.**
proxima, Rachionotomyia.
Pseudococcus lilacinus, effect of bait sprays on natural enemies of, in Kenya, **226.**
pseudosolani, Myzus.
psidii, Pulvinaria.
Psorophora cingulata, in Trinidad, **495.**
Psorophora ferox, in Trinidad, **495.**
Psorophora lineata, in Trinidad, **495.**
Pteronidea leucotrochus, bionomics of, on gooseberry in Br. Isles, **6–10.**
Pteronidea ribesii, bionomics of, on *Ribes* in Br. Isles, **1–6.**
pubescens, Tomaspis.
Pulvinaria psidii, effect of bait sprays on natural enemies of, in Kenya, **226.**
purpuraceus, Aëdes (*Ochlerotatus*).
Pycnosoma rufifacies, in New Zealand, **475.**
pygmaeus, Cephus.
pygophora, Salpingogaster.
Pyrausta nubilalis, Coccinellid predacious on, in Germany, **118.**
Pyrethrum, extract of, in paraffin against *Lygus simonyi*, **96–99.**

Q.

quadrimaculata, Calliphora.
quasiferox, Megarhinus.
quasiluteoventralis, Wyeomyia.
Quercus aegilops (Valonia Oak), relation of breeding-places of *Dociostaurus maroccanus* to, in Anatolia, **277.**

R.

Rachionotomyia aranoides, Megarhinus kempi predacious on, **73.**
Rachionotomyia proxima, larva of, **74.**
ranacea, Cyrtacanthacris (see *C. tatarica*).
repens, Filaria.
rhecter, Aëdes.
Rhembobius abdominalis, parasite of *Merodon equestris* in U.S.A., **441.**
Rhodesia, Southern, new mosquito from, **562.**
Ribes spp., sawflies infesting, in Gt. Britain, **1–15.**
ribesii, Pteronidea.
Rice-fields, mosquitos breeding in, in Trinidad, **486–491.**
rubens, Ceroplastes; *Epineura.*
rubra, Tomaspis.
ruficeps, Geocoris.
ruficornis, Acanthacris.
rufifacies, Pycnosoma.
rufipes, Calliphora; *Pollenia.*
Rumex acetosa, influence of percentage of, on *Smynthurus viridis*, **173.**

S.

Sabethes cyaneus, in Trinidad, **495.**
Sabethes undosus, in Trinidad, **495.**
saccharalis, Diatraea.
saccharina, Tomaspis.
Saissetia spp., **224**; effect of bait sprays on natural enemies of, in Kenya, **226**; parasites of, **223, 225.**
Salpiglossis, food-plant of *Erythroneura parvula*, **42.**
Salpingogaster nigra, life-history of, in Trinidad, **203, 208–210.**
Salpingogaster pygophora, predacious on *Tomaspis rubra* in Trinidad, **210.**
Salvia, food-plant of *Erythroneura* spp., **42.**
Sarcophaga, relations of, to *Lucilia sericata*, **240, 244.**
Sarcophaga froggatti, **45.**
Sarcophaga frontalis, **45.**
Sarcophaga fuscicauda, doubtful identity of, **45.**
Sarcophaga hutsoni, genital characters of, **45, 46.**
Sarcophaga irrequieta, **45.**
Sarcophaga karnyi, genital characters of, **45.**

Sarcophaga misera, **46.**
Sarcophaga peregrina, bionomics of, in Australia, **47 ;** notes on and key to spp. allied to, **45–48.**
Sarcophaga tryoni, **45.**
scabriusculus, Sphingonotus.
scapularis, Aëdes.
Scaurus tristis, **230.**
Schistocerca gregaria, **65, 455 ;** phases and development of, in S. Africa, **401–402 ;** in Turkey, **273.**
Schistocerca gregaria flaviventris, first stage larva of, **52 ;** adult of, **54.**
Sciara, predacious on *Smynthurus viridis*, **175.**
Scilla, food-plant of *Merodon equestris*, **429, 431.**
Scintharista magnifica, in S. Africa, **391.**
Scolytus amygdali, in stone-fruit trees in Palestine, **252.**
scotti, Culex.
Scymnus, **223.**
segmentata, Meta.
Sepimentum demissum, in New Zealand, **475.**
Sepimentum fumosum, in New Zealand, **475.**
septemfasciata, Nomadacris.
septempunctata, Coccinella.
sepulchralis, Isotoma.
sericata, Lucilia.
Seychelles, *Culex scotti* in, **562.**
shillitonis, Uranotaenia.
similis, Stenus.
simonyi, Lygus.
Singa hamata, predacious on *Smynthurus viridis*, **124.**
Skusea, a subgenus of *Aëdes*, q.v.
Smynthurus viridis (Lucerne Flea), ecological study of, in Britain, **101–145, 151–190 ;** geographical distribution of, **181.**
Soda, Caustic, in formula against *Antestia*, **218.**
Sodium Arsenite, in poison bait formula against *Antestia*, **219 ;** experiments with dust of, against *Locusta migratoria migratorioides* in Sudan, **66–68 ;** toxicity of, **455.**
Sodium Fluosilicate, against *Locusta migratoria migratorioides* in Nigeria, **449–461 ;** dusts of, ineffective against locusts, **67.**
solanina, Aphis.
sorghi, Aphis.
Sorghum halepense, food-plant of *Diatraea saccharalis* in tropical America, **268.**
speculator, Stenus.
Sphaerularia, **116.**
Sphex aegyptiacus, attacking *Anacridium moestum melanorhodon* in Sudan, **57.**
Sphingonotus scabriusculus, in S. Africa, **320–321, 390, 391, 403.**
squamosus, Culex.
Stegomyia, a subgenus of *Aëdes*, q.v.
Stellaria media (see Chickweed).
Stenus spp., predacious on *Smynthurus viridis* in Britain, **119, 125, 126.**
Stephanoderes hampei, **223.**
sternalis, Calliphora.
stigmaterus, Microdus.
Stirastoma depressum, Pachira aquatica original food-plant of, **264.**
Stomatoceras micans, parasite of *Glossina* spp. in Nigeria, **466.**
Stomoxys calcitrans (*aenos*), in New Zealand, **473–474.**
strigatus, Eumerus.
stygia, Calliphora.
Stylops, **116.**
subhemisphaerica, Saissetia.
Sudan, bionomics and control of locusts in, **49–64, 65–68.**
Sugar-cane Froghopper (see *Tomaspis saccharina*).
superbus, Megarhinus.
Swede (*Brassica napus*), food-plant of *Myzus persicae* in Br. Isles, **546.**
Syntomosphyrum glossinae, parasite of *Glossina morsitans*, **463.**
Systates, **223.**

T.

tachinoides, Glossina.
Taeniorhynchus (*Mansonioides*) *annulatus*, chitinisation of larvae of *Microfilaria malayi* in, **230.**
Taeniorhynchus (*Mansonioides*) *annulipes*, **230.**
Taeniorhynchus (*Mansonioides*) *uniformis*, in Batavia, **72.**
taitensis, Musca.
tarsimaculatus, Anopheles.
tatarica, Cyrtacanthacris.
Telenomus truncativentris, parasite of *Antestia lineaticollis* in Kenya, **217.**
Temperature, effect of, on development of *Smynthurus viridis*, **135–138, 140–142, 154–168.**
Teosinte (see *Euchlaena mexicana*).
tessellata, Bez., *Calliphora* (see *C. bezzii*).
testacea, Uranotaenia.
theileri, Trypanosoma.
Theobaldia atlantica, sp. n., from Azores, **560.**
Theobaldia maccrackenae, **561.**
Thliptoceras octoguttalis (Coffee Berry Borer Moth), parasites of, in Kenya **223, 225.**

Thyridanthrax abruptus, parasite of *Glossina*, **463.**
Thyridanthrax argentifrons, parasite of *Glossina* in Nigeria, **463, 466, 467.**
Tibellus oblongus, predacious on *Smynthurus viridis*, **123, 125, 184.**
tibialis, Calliphora.
tomaspidis, Abbella.
Tomaspis bodkini, in Orinoco Delta and Br. Guiana, **270.**
Tomaspis pubescens, Syrphid enemy of, in Trinidad, **210 ;** food-plants of, in Br. Guiana, **270.**
Tomaspis rubra, Syrphid enemy of, in Trinidad, **210.**
Tomaspis saccharina (Sugar-cane Froghopper), original habitat of, in tropical America, **270 ;** natural enemies of, in Trinidad, **203–210.**
Tomato, food-plant of *Erythroneura parvula*, **42.**
Toxoptera aurantii, **224 ;** effect of bait sprays on natural enemies of, in Kenya, **226.**
Trachygnatha dentata, predacious on *Smynthurus viridis*, **123.**
tragelaphi, Trypanosoma.
transversalis, Merodon equestris.
Tricholaena rosea, food-plant of *Diatraea saccharalis* in tropical America, **268.**
trichopygus, Megarhinus.
Trifolium repens, food-plant of *Smynthurus viridis* in England, **104.**
Trinidad, natural enemies of *Tomaspis saccharina* in, **203–210 ;** food-plants of sugar-cane pests in, **260–262, 269–270 ;** physico-chemical factors of water in relation to mosquito breeding in, **477–496 ;** list of mosquitos in, **494–495.**
trinidadensis, Megarhinus ; Phlebotomus.
Trioza viridula, Coccinellid predacious on, in Latvia, **118.**
tristis, Scaurus.
truncativentris, Telenomus.
tryoni, Sarcophaga.
Trypanosoma spp., infesting cattle in the Gold Coast, **502, 503.**
Tsetse-flies (see *Glossina* spp.).
tuberculatus, Eumerus.
Tulip, occasional food-plant of *Merodon equestris*, **431.**
Tychea phaseoli (see *Geoica*).
Typhlocyba, **116.**

U.

Uganda, new mosquitos from, **561–562.**
umbratica, Epeira.
undecimpunctata, Coccinella.
undosus, Sabethes.
uniformis, Taeniorhynchus (*Mansonioides*).
United States of America, *Rhembobius abdominalis* parasitising *Merodon equestris* in, **441.**
Uranotaenia candidipes, **561.**
Uranotaenia geometrica, in Trinidad, **495.**
Uranotaenia hopkinsi, sp. n., from Uganda, **561.**
Uranotaenia lowii, in Trinidad, **495.**
Uranotaenia macfarlanei, larva of, **74.**
Uranotaenia shillitonis, sp. n., from Uganda, **561.**
Uranotaenia testacea, larva of, from Hong Kong, **559.**
urichi, Anagrus.

V.

validus, Merodon equestris.
Vallota, food-plant of *Merodon equestris*, **431.**
Valota insularis, food-plant of *Diatraea saccharalis* in tropical America, **268.**
variegatus, Aëdes (*Stegomyia*).
varioannulatus, Culex (see *C. pipiens*).
Venezuela, food-plants of sugar-cane pests in, **263–270.**
Verbena, Lemon-scented, food-plant of *Erythroneura parvula*, **42.**
verrucarum, Phlebotomus.
vicaria, Musca (see *M. domestica*).
violacea, Calliphora.
violaceus, Perilampus.
viridis, Isotoma ; Smynthurus.
viridula, Trioza.
Vitex cienkowskii, relation of *Glossina* to, in the Gold Coast, **506, 511, 519–524, 529.**
vivax, Trypanosoma.
Volumnus obscurus, on coffee in Kenya, **85.**

W.

Water, Hot, treatment of bulbs with, **443.**
wickhami, Ceratophyllus.
Wyeomyia bromeliarum, in Trinidad **495.**
Wyeomyia quasiluteoventralis, in Trinidad, **495.**

X.

Xanthium pungens, *Euaresta aequalis* ovipositing on, **191–193.**
Xantholinus cephalus, predacious on *Ips pini* in America, **120.**
Xantholinus hamatus, predacious on *Chortophila brassicae* in Canada, **120.**
Xantholinus linearis, predacious on *Smynthurus viridis*, **120.**
Xenopsylla astia, methods of rearing, **25.**
Xenopsylla cheopis, methods of rearing, **25.**
Xysticus, predacious on *Smynthurus viridis*, **123, 125, 184.**
Xysticus cristatus, **123, 184.**

Z.

zimmermannii, *Lephthyphantes*.
Zizyphus spina-christi, locust larvae feeding on, **56.**
Zygina (see *Erythroneura*).

INDEX TO NAMES OF PERSONS.

Aarons, —, **258.**
Abbiss, —, **445.**
Anderson, T. J., **99, 228.**
Andrewartha, W., **551.**
Aragão, H. de Beaurepaire, **19.**
Atif Bey, **273.**

Balfour-Browne, J., **560, 561.**
Barker, H. D., **257, 258.**
Beadle, L., **562.**
Beattie, M. V. F., **477.**
Beaurepaire Aragão, H. de, **19.**
Bère, Lach de, —, **75.**
Bodkin, G. E., **255.**
Bonne-Wepster, J., **69, 233.**
Bosman, L. D., **298.**
Boughton, I. B., **258.**
Box, H. E., **258, 260.**
Brain, C. K., **339.**
Bremekamp, C. E. B., **334.**
Brèthes, J., **22.**
Bristowe, W. S., **189.**
Britten, H., **35.**
Broadway, W. E., **257.**
Brug, S. L., **73, 229.**
Brumpt, E., **17, 19, 23.**
Buckley, T. A., **196.**
Buxton, P. A., **17, 189.**

Chevallier, A., **258.**
China, W. E., **34, 35.**
Cleare, L. D., **258.**
Coldham, P. J., **99.**
Colvin, C., **258.**
Cooper, —, **526.**
Cornelis, M., **79.**
Currie, G. A., **191.**

Dardeau, W., **258.**
Dash, J. S., **257.**
Davies, W. M., **535.**
Davis, —, **258.**
Davson, Sir E., **257.**
de Loor, B., **298.**
de Rippas, P., **105, 189.**
de Rook, H., **76, 78, 79, 81, 82.**
de Vries, A. H., **298.**
Dietz, —, **258.**
Dolge, R., **258.**
Doyne, H. C., **460.**
Dozier, H. L., **258.**
Drew, D., **562.**

Eccles, —, **257.**
Edwards, F. W., **73, 495, 559.**
Ekman, —, **257.**
Eraso, E., **258.**
Evans, A. M., **561.**

Farrar, C., **257.**
Faure, Jacobus C., **293.**
Ferrière, C., **206, 207.**
Field, M., **298.**
Fuat Bey, **273.**

Golding, F. D., **449.**
Gomez, J. V., **258.**
Gordon, J. R. C., **257.**
Grabham, M., **560.**

Haidar Bey, **273.**
Hardy, G. H., **45, 549.**
Hargreaves, H., **562.**
Harris, W. V., **298, 342.**
Hebert, C., **258.**
Hodson, W. E. H., **247, 429.**
Holmes, E. T., **460.**
Hopkins, G. H. E., **561, 562.**

Immelman, M. N. S., **298.**
Imms, A. D., **189.**

Jack, R. W., **298, 344.**
Jackson, R. B., **559.**
Janse, A. J. T., **298.**
Jeffery, R. C., **189.**
Johnston, H. B., **49, 298, 345.**
Jolles, P., **251.**

Kelly, S. G., **191.**
King, H. H., **65.**

Kozlovsky, S., **189.**
Krause, H., **278** (note).

Lach de Bère, —, **75.**
Lane, R. E., **94.**
Lea, H. A. F., **298.**
Leeson, H. S., **25, 562.**
Leonard, L. Y., **258.**
Le Pelley, R. H., **85, 217.**
Long, A. W. B., **258.**
Loor, B. de, **298.**

McConnell, R. E., **562.**
MacGill, E. I., **33.**
Mackerras, I. M., **551, 553.**
Mackie, J. R., **460.**
MacLagan, D. S., **101, 151.**
Magowan, J. H., **258.**
Marais, S. J. S., **298, 329, 387.**
Marshall, Sir G. A. K., **189, 518.**
Maule, J., **460.**
Mayo, J. K., **460.**
Mazza, S., **17, 19, 21, 22.**
Medina, M., **258.**
Mer, G., **563.**
Miles, H. W., **1, 35.**
Miller, D., **469.**
Miller, N. C. E., **195.**
Morris, K. R. S., **501, 518.**
Myers, J. G., **102, 123, 125, 203, 210, 257.**

Naudé, T. J., **298, 339, 387.**
Neethling, P. C., **298.**
Newman, L. J., **183.**
Nicholson, A. J., **193.**

Oakley, H. B., **68.**
Oakley, P., **531.**
Oosthuizen, M. J., **298.**
O'Reilly, W. E., **258.**

Pacannis, —, **258.**
Penãs, R., **258.**
Pendlebury, H. M., **198.**
Pickles, A., **203.**
Pittier, H., **257, 258.**
Pomeroy, A. W. J., **501.**
Powell, W., **298.**

Quayle, H. J., **328.**

Requena, R., **258.**
Richardson, T., **35.**
Rippas, P. de, **105, 189.**
Ritchie, A. H., **298.**
Rodman, G. H., **35.**
Rodriguez, —, **481.**
Röhl, E., **258.**
Rook, H. de, **76, 78, 79, 81, 82.**
Ruttledge, W., **65.**

Salt, G., **211, 235.**
Schaefer, E. E., **298, 371.**
Schweickerdt, W. J., **334.**
Shevket Bey (Nihat), **273.**
Shillito, J. F., **561, 562.**
Snijders, —, **233.**
Son, G. van, **336, 337, 339, 391.**
Squire, F. A., **298.**
Stoy, R. H., **211, 213, 215.**
Sullivan, —, **258.**
Sureya Bey, M., **273.**

Taylor, A. W., **463.**
Tevfik Bey, **273, 280** (note).
Theodor, O., **17.**
Thompson, W. R., **102, 176, 185, 189.**
Thomsen, F., **339.**
Tiegs, O. W., **556.**
Tillyard, R. J., **191, 193.**

Urich, F. W., **206, 210.**
Uvarov, B. P., **273, 298, 460.**

van Son, G., **336, 337, 339, 391.**
van Zyl, B., **340, 342.**
Vicentini, C., **258.**
Vigne, C., **518.**
Voss, V., **334.**
Vries, H. de, **298.**
Vuillet, J., **57.**

Walker, —, **258.**
Whitfield, B. W., **68.**
Whitfield, F. G. S., **68.**
Whitney, —, **258.**
Wigglesworth, V. B., **463.**
Williams, L., **518.**
Williams, R. O., **257.**
Wilson, F., **240.**
Wilson, G. F., **35.**
Wise, K. S., **23.**
Wright, C. H., **457, 460.**

Yãnes, —, **258.**

Zolotarevsky, B. N., **298.**
Zyl, B. van, **340, 342.**